A SYSTEMATIC REVISION AND THE EVOLUTIONARY BIOLOGY OF THE *PTOMAPHAGUS* (*ADELOPS*) BEETLES OF NORTH AMERICA (COLEOPTERA; LEIODIDAE; CATOPINAE), WITH EMPHASIS ON CAVE-INHABITING SPECIES[1]

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ABSTRACT. The subgenus *Adelops* of the genus *Ptomaphagus* of the New World is revised; figures and descriptions are given for 36 species. Seventeen new species and subspecies of *Adelops* are described: *loedingi julius, loedingi solanum, barri, hazelae, fiskei, walteri, episcopus, cocytus, cavernicola aditus, gypsum, oaxaca, jamesi, altus, newtoni, leo, meximontanus,* and *talamanca*. Twelve new synonymies and new combinations in *Adelops* are recognized.

In the higher categories containing *Ptomaphagus* a conservative classification uses the taxa Leiodidae, Catopinae, Ptomaphagini, and Ptomaphagina. The genus *Echinocoleus* is transferred from the tribe Nemadini to the tribe Ptomaphagini. *Adelops mitchellensis* Hatch is transferred to the genus *Adelopsis* in the Ptomaphagina.

Five ecological categories of habitat specialization hold the species of *Adelops*: forest litter inhabitants, animal burrow and nest inhabitants, soil inhabitants, troglophiles, and troglobites. The biology is discussed, especially that of cave specialization in *Adelops* (progressive and regressive changes), in adults and larvae, and is compared with the Bathysciini.

A phylogeny and zoogeography is proposed for the tribe, and for the species of *Adelops*. These are discussed in detail for the cave species. It is found that many independent cave colonizations occurred in the United States, Mexico, and

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[1] This paper is based on a thesis presented to the Department of Biology, Harvard University, in partial fulfillment of the requirements for the Ph.D. degree.

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Guatemala in the later half of the Pleistocene which produced a total of 19 troglophilic and troglobitic species.

PREFACE

This work began in the spring of 1964 when, as a senior studying under Dr. Thomas C. Barr at the University of Kentucky, I learned of a large unworked collection of several thousand *Ptomaphagus* beetles collected by Dr. Walter B. Jones in caves in Alabama. This collection was assembled by Dr. Jones from the early 1930's to the late 1940's, and was deposited in the Alabama Museum of Natural History. It had been partly studied by Dr. Milton W. Sanderson and Dr. Albert Miller, both then at the University of Arkansas. Because Drs. Sanderson and Miller were forced by other obligations to give up their study of the collection, it lay unworked until it was transferred to Dr. Barr and finally to me.

The Jones collection, combined with my collections and those of Dr. Barr, was the basis of a revision of the systematics of the cavernicolous *Ptomaphagus* of the United States, presented as a Masters Thesis in 1966 to Northwestern University, under the direction of Professor Orlando Park. In that work 3,965 specimens were examined of 14 facultatively and obligately cavernicolous species from 149 localities. Of these, 3,194 specimens from 109 caves in the eastern United States were considered to belong to 11 troglobitic (obligately cavernicolous) species.

Since 1966 work has continued on the systematics and biology of the cave-inhabiting species. The present work recognizes 12 species of troglobites in the eastern United States (of which 5,621 specimens have been examined from 177 cave localities), one species of troglobite from Arizona, two from Mexico, and one from Guatemala. The study has been broadened to encompass the systematics and some aspects of the evolutionary biology of the epigean as well as the hypogean species of the entire subgenus *Adelops*, which ranges from its southern distributional limit in Panama northward to its northern limit in southern Canada. I have supplemented museum and laboratory work with a total of more than five summer seasons of field observations and collecting from 1965 to 1969. One field season was spent in Costa Rica and Panama, and a second in Mexico and Guatemala. Three were spent in the eastern United States, primarily in the Cumberland Plateau region of Alabama and adjacent states. Two weeks each were spent collecting in Puerto Rico and Jamaica.

The work was presented as a Ph.D. thesis to Harvard University in 1970, and was put in final form while I was a Postdoctoral Fellow at Carleton University.

INTRODUCTION

Of all the New World beetles in the family Leiodidae *sensu latu,* I believe that the genus *Ptomaphagus* has the most interesting and complex evolutionary story to tell. The family is generally composed of small, secretive, and drab species, which, with few exceptions, possess the family hallmark of antennae having the eighth segment noticeably smaller than the seventh and ninth. The family occupation is scavenging. Members are generally found in association with decomposing organic material such as humus, carrion, dung, and fungi, and they dwell primarily in moist and forested environments. These habits are consistent around the world. Some species have become specialized scavengers as guests in social insect nests, and others may frequent terrestrial vertebrate nests and burrows.

Frequently, in the work to follow, *Ptomaphagus* and the tribe Ptomaphagini will be compared to, and contrasted with, beetles in the tribe Bathysciini (both in the Catopinae). The Bathysciini are remarkable, and are presently the best generally known group of Leiodidae. They display both great ecological restriction and great phyletic diversification. All but one of the

121 genera and two of the 583 species (Lanyrie, 1967, 1969) are limited to the Palearctic region. The exception is the myrmecophilous and termitophilous *Platycholeus* of California and Washington. All species have lost their flight wings, and all are eyeless except a dozen or so. Their restriction lies in their need for cool moist habitats. A review of the Bathysciini (Lanyrie, 1967) found that in 883 recognized valid species and subspecies, 81 percent are troglobites dwelling in European caves, 10 percent are humus inhabitants in Palearctic forests, and 7 percent are soil inhabitants of the same forests.

In contrast to the Bathysciini, the Ptomaphagini exhibit greater ecological versatility, but less phyletic diversification. The Ptomaphagini are more widely distributed over much of the Old and New Worlds and occupy a greater variety of habitats. But evolutionary diversification has not resulted in as many genera or species. Excluding *Ptomaphagus,* the tribe contains six genera with 50 valid species. Two genera occur in Indo-Malayan forests, two occur only as myrmecophiles (one in north Africa, and one in the southern United States), one genus is an inhabitant of forests and caves in the West Indian Islands and Mexico, and the last is an inhabitant of caves and forest litter in North and South America.

Ptomaphagus is recognized as containing four subgenera. Two are each composed of two species, limited to the Balkans, and to Mexico and Brazil. The subgenus *Ptomaphagus* is Palearctic, containing 22 species found mostly in forested habitats, but also in nests of ants, terrestrial vertebrates, and occasionally in caves. No cave-adapted species are known. The subgenus *Adelops,* the primary subject of this work, is known in the New World from Panama to southern Canada. This paper treats 36 species of *Adelops* as valid, and leaves undescribed a tentative number of seven species from Mexico and Guatemala that are known from inadequate material.

Adelops is ecologically the most versatile group of New World Leiodidae. Most species are fully eyed and winged, with large ranges. These ranges comprise much of the mesic deciduous forests of the eastern United States and Canada. They are inhabitants of the litter on the forest floor, and occasionally the nests and burrows of mice, pocket gophers, and gopher tortoises. The western species often have wide ranges in the more xeric portions of North America, and are more frequently found in association with nests and burrows of *Pogonomyrmex* harvesting ants, prairie dogs, pocket gophers, pack rats, and burrowing owls.

Some described and undescribed Mexican and Central American species are inhabitants of mesic forests at middle and high elevations. They are absent from lowland tropical forests.

In a discussion of phylogeny and zoogeography it is proposed that a Tertiary specialization to forest litter habitats probably resulted in a loss of wings and a reduction of eyes in some species. Under conditions of fluctuating Pleistocene climates some of these specialized species evolved into a suite of 16 cave-specialized (troglobitic) species in the southeastern and southwestern United States and in Mexico and Guatemala. The cavernicolous species display a series of morphological changes in eyes and appendages that reflect various stages of adaptation to cave habitats. In contrast, although other New World Leiodidae do occur in most, or at least many, of the habitats occupied by *Ptomaphagus,* none are known that have invaded and become specialized to caves.

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and 1968–1969 was supported by NSF grants GB 3167 and GB 7346 respectively, to the Evolutionary Biology Committee, Harvard University, Professor Reed C. Rollins, principal investigator. Additional funds for field work were made available by the R. W. Stone Award of the National Speleological Society, the Field Museum of Natural History, Museum of Comparative Zoology, American Museum of Natural History, and by individuals, including W. B. Muchmore, T. C. Barr, Henry Howden, Theodore Hubbell, W. L. Brown, and Ralph Crabill.

I was assisted in the field work by many people, all of whom are thanked. Most notable of these are Alan Fiske who helped in the summer of 1967, James Peck in the summers of 1965 and 1969, and Russell Norton in the summer of 1969. Dr. and Mrs. W. B. Jones of Huntsville, Alabama, are warmly thanked for providing a central location for many months of field work in Alabama and adjoining states. I have also been helped with collections from Bill Torode, Dick Graham, Tony Iles, John and Martha Cooper, John Holsinger, Art Dobson, and many others. James Reddell, William Elliott, and other members of the Texas Speleological Survey and the Association for Mexican Cave Studies are especially thanked for providing material from Texas and Mexico.

Drs. Barbara Warburton of Texas Southmost College, Brownsville, Texas, and Thomas C. Barr, University of Kentucky, are thanked respectively for use of the Rancho Del Cielo, Mexico, and Mammoth Cave, Kentucky, field stations under their direction.

The extensive collections of the Museum of Natural History of the University of Alabama were assembled by Dr. W. B. Jones, who was frequently accompanied in the field by J. M. Valentine, A. B. Flannigan, H. P. Loding, A. F. Archer, and L. Hubricht. The extensive cave collections of Thomas C. Barr were contributed to by Leslie Hubricht, H. R. Steeves, Jr., and others. Walter Suter and H. R. Steeves, Jr. provided extensive material, deposited in the FMNH, from their Berlese funnel collections from forest litter. Other collectors and collection curators helping in my study are acknowledged in the list of collections. I regret that space is not available to name every collector individually.

The owners of the caves investigated in this study, as well as the speleologists who gathered helpful cave information, are too numerous to mention, but a debt is owed to each. Special help with cave information was provided by Thomas C. Barr, William W. Varnedoe, Russell Gurnee, and Bill Torode.

Professor F. M. Carpenter of the Biological Laboratories, Harvard University, provided much-needed assistance in administrative matters and details of fieldwork funding. Professor P. J. Darlington, Jr., Dr. John F. Lawrence, and others from the Museum of Comparative Zoology, Harvard University, offered welcome advice and assistance on many matters of procedure and operation. The completion of the work at Carleton University was made possible under a systematic operating grant to Dr. H. F. Howden from the National Research Council of Canada.

Some of the drawings, and other forms of encouragement and aid, were provided by my wife Jarmila.

METHODS AND MATERIALS

In this study I have examined more than 9,800 specimens of North American *Ptomaphagus*. About 70 percent of this number represents 12 troglobitic species of the eastern United States, and two troglophilic species from the United States and Mexico. The large numbers of cave-collected specimens (contrasted to epigean specimens) represent (1) the greater collecting emphasis that has been placed on caves, (2) the greater ease of collecting a large series from cave populations, (3) the

elusive nature or scarceness of the epigean species, and (4) the special collecting techniques needed by, and the beetles' unexciting appearance for, a general epigean beetle collector.

The following list indicates the private and institutional collections and curators from which specimens were borrowed, and the abbreviations (after Arnett and Samuelson, 1969) for these collections used in the paper.

AMNH	Department of Entomology, American Museum of Natural History, New York, New York 10024. L. Herman, Jr.
ANSP	Department of Entomology, Academy of Natural Sciences, Philadelphia, Pennsylvania 19103. M. G. Emsley.
BMNH	British Museum (Natural History), Cromwell Road, London, S.W.7, England. P. M. Hammond.
CAS	Department of Entomology, California Academy of Sciences, San Francisco, California 94118. H. B. Leech.
CCC	Claude Chantal collection, 425 St-Olivier, Quebec 4, Quebec.
CNCI	Canadian National Collection of Insects, Entomology Research Institute, Ottawa, Ontario. H. Howden, J. M. Campbell.
CUIC	Cornell University Insect Collection, Department of Entomology, Cornell University, Ithaca, New York 14850. L. L. Pechuman.
ENCB	Escuela Nacional de Ciencias Biologicas, Instituto Polytecnico Nacional, Mexico 17, D. F., Mexico. C. Bolivar y Pieltain.
FMNH	Field Museum of Natural History, Chicago, Illinois 60605. H. Dybas, R. Wenzel.
FSCA	Florida State Collection of Arthropods, Florida Department of Agriculture, P. O. Box 1269, Gainesville, Florida 32601. R. E. Woodruff.
GHNC	G. H. Nelson, Kansas City College of Osteopathy and Surgery, 2105 Independence Avenue, Kansas City, Missouri 64124.
HAHC	Henry and Anne Howden Collection, Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada.
INHS	Illinois Natural History Survey, Urbana, Illinois 61803. M. Sanderson.
JHSC	Jorge Hendrichs S., Apdo. Postal 11–774, Mexico 11, D. F., Mexico.
KS	Karl Stephan, 3038 E. Eastland Street, Tucson, Arizona 85716.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138. P. J. Darlington, Jr., J. F. Lawrence.
MNHN	Museum National d'Histoire Naturelle, Laboratoire d'Entomologie, 45 bis, rue de Buffon, Paris V^{e}. M. A. Villiers.
NR	Naturhistoriska Riksmuseet, Entomologiska Avdelningen, 104 05 Stockholm 50, Sweden. T. Nyholm.
NYSM	New York State Museum and Science Service, Albany, New York 12224. J. A. Wilcox.
PISZ	Polish Institute of Systematic Zoology, Slakowska 17, Krakow, Poland. W. Szymczakowski.
PURC	Purdue University Entomology Research Collection, Department of Entomology, Lafayette, Indiana 47907. R. H. Arnett.
SEMC	Snow Entomological Museum, University of Kansas, Lawrence, Kansas 66044. G. Byers.
SBP	Stewart B. Peck, Department of Biology, Carleton University, Ottawa 1, Ontario, Canada.
TCB	Thomas C. Barr, Department of Zoology, University of Kentucky, Lexington, Kentucky 40506.

TAMU Department of Entomology Collection, Texas A & M University, College Station, Texas 77843. H. R. Burke.

UANH Museum of Natural History, University of Alabama, Box 5897, University, Alabama 35486. H. Boschung.

UBCZ Spencer Entomological Museum, Department of Zoology, University of British Columbia, Vancouver 8, British Columbia, Canada. G. G. E. Scudder.

UMMZ University of Michigan Museum of Zoology, Ann Arbor, Michigan 48104. R. D. Alexander.

USNM United States National Museum, Smithsonian Institution, Washington, D. C. 20560. P. J. Spangler, J. M. Kingsolver.

VMKC Vernon M. Kirk Collection, USDA, Northern Grain Insects Research Laboratory, University Station, Brooking, South Dakota 57006.

When sufficient numbers are available paratype and representative specimens of material from my collections are placed in the following collections in the order indicated: SBP, MCZ, TCB and UANH for cave species, USNM, FMNH, AMNH, CAS, CNCI, BMNH, JHSC, ENCB for Mexican and Guatemalan species.

Localities of specimens were determined from labels with the specimens. These localities are given for each species alphabetically, by country, state or province or department, and county in that order. More exact localities are listed after the county, with reference to human settlements and sometimes habitat in parentheses. Distance from settlements and elevations are recorded as on the labels and are not here uniformly changed into the English or the metric system. Variations result from the various maps and instruments available to the different collectors, and whether a distance is taken as road or airline. Localities that cannot be found on maps and atlases available to me and placed in a county are placed at the end of the state list. Material with only state locality is not used. Unlocatable localities are not indicated on the distributional maps. The number of specimens from the locality precedes the parentheses enclosing the abbreviation of the collection in which the particular specimens are located.

Cave locations are generally available only from special publications. I know of the following published surveys concerning areas from which cave-inhabiting *Ptomaphagus* are known to occur: Alabama (Tarkington, Varnedoe, and Veitch, 1965; Jones and Varnedoe, 1968); Guatemala (Gurnee, 1968); Illinois (Bretz and Harris, 1961); Mexico (Russell and Raines, 1967); Missouri (Bretz, 1956); and Tennessee (Barr, 1961a). In Alabama, in a few possibly confusing situations regarding cave names, the name is accompanied by the number of that cave in the Alabama State Cave Survey. I have coined a few names for caves in Tennessee that are not listed by Barr, basing the name on a nearby, named, prominent, topographic feature.

Field Methods

The secretive nature and substrate occupation of *Ptomaphagus* do not lead to easy collecting. Occasional specimens may be found in forest litter, or mammal nests, or in caves. The large series of specimens required for careful population study demands the use of mass collecting techniques. These are baited pitfall traps, and Berlese funnels.

Traps and baiting. The use of baited pitfall traps has been a long-suggested method of collecting terrestrial arthropods. The method has the advantage that it can concentrate a normally dispersed fauna, and then capture and retain the individuals until the investigator has the opportunity to revisit the site. Many techniques of trapping are given in Southwood (1966). A

technique of trapping in caves has been described by Barber (1931).

The traps I used in caves from 1965 to 1968 were modified from those of Barber. A plastic cup, without a handle, with a volume of about 3/4 of a pint, was sunk in the floor of the cave in an area suspected to harbor *Ptomaphagus*. Into the cup was poured a 1/2-inch depth of Galt's solution (1 part KNO_3, 1 part chloral hydrate, 5 parts NaCl, dissolved in 100 parts water, all by weight). This salt solution narcotized and drowned the insects, and then retarded decay for over one month. Over the mouth of the trap was placed a square of 1/4-inch mesh hardware cloth, which kept out such large animals as crickets. From the hardware cloth the bait was suspended by a wire so that it hung in the cup above the solution. A large flat rock over the trap was necessary to prevent vertebrate predators and scavengers from stealing the bait. The best bait for trapping cave *Ptomaphagus* was found to be a piece of decayed hog liver or human dung wrapped in a piece of gauze. Similar small traps can be used in animal burrows (gopher tortoise or pocket gopher) or at the entrance to animal dens, all preferably after the vertebrate occupant is removed. These small traps (unbaited) also work on the mounds of *Pogonomyrmex* harvester ants (Melander, 1902).

Larger versions of these traps (using empty number 10 cans) were used extensively in forests in the United States, Mexico and Central America, and the West Indies. Here, the better bait seemed to be human dung. Carrion would attract *Ptomaphagus* only infrequently and unpredictably.

From 1968 to 1970 the fluid used in the traps was water with a small amount of liquid detergent, the salt solution being judged unnecessary. In 1971, in over four months of work in Venezuela, El Salvador, Mexico, and the southeastern United States, I found that an even better trap came into either the carrion or dung. How-fluid is a 50/50 mixture of water and laboratory grade ethylene glycol.

The use of baits, without traps, never gave satisfactory results in forests. It was too difficult to collect any beetles that ever, in caves baiting without traps is a very effective way of attracting the beetles. In several cases, a cave known to be inhabited by *Ptomaphagus* would be searched and none would be found. In such caves, a few pieces of carrion or dung bait placed under rocks in the cave would attract from several to hundreds of beetles within a week. When working on the edge of a species range, baiting is a useful technique to determine if the cave is populated with *Ptomaphagus*. If repeated baiting does not draw the beetles, it is safe to conclude that the cave is not occupied, and is outside the species range.

Berlese funnels. Many specimens of *Ptomaphagus* have been taken by me and others using funnels with the Tulgren modification (see Southwood, 1966: 144). Litter samples were taken from open forest floors, stump holes, root buttresses, and litter accumulations on the uphill sides of logs. The leaves, humus and soil were sifted in the field through a 1/2-inch mesh screen to remove unrotted leaves, stones, and sticks. The sifted debris was carried and stored in large plastic bags (holding 20–30 pounds) until it could be placed in the funnels. The litter was sifted a second time just before being placed in the funnels. When processed, three liters of litter were placed in each funnel (45 cm high, 30 cm across the top, with the screen 10 cm from the top) on a double layer of cheesecloth supported by the screen. A 60-watt bulb was used over the litter. Two thin wood or cardboard strips separated the top of the funnel from the rim of the bottom funnel and provided ventilation and allowed the escape of excess moisture. Samples were changed at 12-hour intervals. During the periods of maximum operation, up to 24 funnels were used, each holding

three-liter samples of litter for 12 hours. In this way up to 144 liters of litter could be extracted in each 24-hour period. The magnitude of this collecting is expressed in the following figures. In 1967 I Berlese-extracted the fauna from 3114 pounds (net weight) of sifted litter (2884 liters) from the eastern United States; in 1968, 4401 pounds (4530 liters) from the eastern United States and 192 pounds (199 liters) from Jamaica; in 1969, 1005 pounds (1090 liters) from the eastern United States and 1224 pounds (1312 liters) from Mexico; and in 1970, 152.7 kg (407 liters) from the eastern United States. This is a total of a minimum of 4664 kg (10,422 liters) of litter processed in the term of field work since I began to keep records. The residues of these collections have been deposited in the FMNH.

The arthropods extracted in this way fell into 70 percent alcohol preservative. All other collections were preserved in "Barber's Fluid" (Valentine, 1942). Barber's Fluid does not harden the tissues of the beetles as does alcohol. The soft and flexible tissues allow easy dissection of the male and female internal genitalic structures that are so important in species recognition. With Barber's Fluid preservation, a beetle's appendages can be manipulated into a position for maximum visibility of critical features before mounting on a point.

Laboratory Methods

Cleaning. Freshly collected and preserved specimens as well as old, dry museum specimens are frequently covered with grease, and adhering debris. Specimens were often cleaned in an E/MC Corp. ultrasonic cleaner in 95 percent ethyl alcohol. However, this may result in the breaking off of some of the apical antennal segments. Dry-pinned material was softened for dissection in boiling water.

Dissections. Dissections were made with insect pins. Dissections are easily performed on material preserved in Barber's Fluid because the genital aperture may be easily opened, the genital structures may be easily hooked, and the aedeagus everted or the spermatheca extracted with a pin or minuten needle. This is not the case for material that is pointed and dried. After they have relaxed in boiling water, the last four segments of the abdomen are usually removed from the specimen in 95 percent alcohol. The specimen is repointed and the abdomen dissected for the aedeagus. Dissecting the abdomen in search of the very fragile female spermatheca is risky in previously dried material. The safest procedure is to place the separated end of the abdomen in a hot KOH solution, and to thus dissolve the tissues away from the spermatheca. The KOH treated material was then washed in water acidified with glacial acetic acid.

Mounting. Aedeagi were observed free in alcohol, on temporary glycerine mounts, and early in the study, on permanent slides made with water soluble "Down's Medium" (polyvinyl lacto-phenol clearing medium; Barr, 1961b). Interpretation of permanent slides must be made with caution because distortion can result from the pressure of the cover glass. Female spermathecae were examined in alcohol or as temporary glycerine mounts. All structures removed in dissections were placed in a small polyethylene microvial (obtained from Arthropod Specialties Co., Sacramento, Calif.) with a drop of glycerine and the plastic plug of the vial was fastened to the pin under the specimen.

The specimens not stored in Barber's Fluid were mounted on stiff paper points on insect pins. The adhesive used was an ethyl alcohol soluble plastic compound called "Elvar," made by Dupont. The mounting point, with the tip bent at a 45-degree angle, was touched to the right side of the specimen's mesosternum. Customary labelling procedures followed.

Illustrations. Drawings of antennae, aedeagi, and genital segments were made by tracing projections of glycerine mounts.

Antennae were oriented so that the drawing represents the broadest outline. Parameres and setae are omitted from aedeagal drawings because these do not add to the value of the drawing. Drawings of spermathecae and dorsal views of aedeagal tips were made with an ocular grid and squared paper. Measurements of antennal segments, pronotum, elytra and eyes were made with a calibrated ocular micrometer in a Leitz stereoscopic microscope, with proportions calculated with a slide rule. Other proportions are visual estimates.

Determination procedure. As material became available to me I tentatively identified it by using existing keys and descriptions, and later, I grouped each tentative species into sets representing local populations, using label information. I compared the sets within themselves and between themselves, using the traditionally important characters of antennal segment proportions, shape of the female elytral apex, and the male aedeagus. I did not find these to give unequivocal results. Continued study of structures within populations showed that characters of equal or greater value lay in the mesosternal carina and its notch in the cave species, the genital segment of the male with its sternite (spiculum gastrale) and two lateral pleurites (genital plates), and the shape of the chitinized female spermatheca. At the end of the study I concluded that the generally most valuable single character for species recognition was the female spermatheca. I know of its previous utilization only in three species of *Ptomaphagus* in Great Britain (Kevan, 1963).

I have found *Adelops* species to be delimited by recognizable morphological discontinuities. In all cases but one the "gap" involves the shape of the spermatheca and at least one character on the male aedeagus or genital plate. I have found these characters to be consistent within populations. Populations are considered to be conspecific if they are from the same or different geographical localities and their genitalic morphology is identical, or if they show intergradation of differences in internal or external characteristics (when present) in geographically neighboring areas. Populations are judged to represent different species in the same or different geographical localities if they differ in genitalic morphology and at least one external character, and do not display intergradation. Problems, however, result in the application of these criteria in separating *nevadicus* and its "*piperi* form" and in the spermathecal variation in *hatchi,* and *brevior.*

Subspecies have been used sparingly, and then only with a few cave-limited species. They represent populations that (1) differ in a few characters, mainly minor differences in the spermatheca, and (2) are also judged to be separate evolutionary units owing to isolation of a geologic or physiographic nature from other populations of the species.

Measurements. These have been sparingly used. They are not judged to be of great importance in diagnosis and determination of *Adelops.* The lengths and widths are from individuals that appeared to the unaided eye to represent the limits of the ranges of size variation. The total length is the chord of the arc from the reflexed head to the elytral apex. The ratios of pronotal and elytral lengths to widths are from small samples judged to be representative of the species. The elytral length was measured as the chord of the arc from the tip of the scutellum to the elytral apex.

BIOLOGY

Many of the general aspects of the biology of *Adelops* have been summarized in the introduction to this work. Specific details are found in the systematic revision in the notes on each species. This includes generalizations about habitats and seasonality. The present section will consider the biological and evolutionary modifications of morphology, anatomy, and behavior.

Life cycle data will be presented in a later paper. The emphasis will be upon comparing and contrasting the epigean and the hypogean *Adelops*, and then in comparing and contrasting the *Adelops* with the Bathysciini. More comparative information exists for the biology of the highly specialized bathysciines than for all the rest of the Catopinae combined. Community and population biology will be treated separately in a later paper. Brief data on the life cycle and ecology of some cave species is in Peck, 1967a and 1967b.

For the sake of clarity in the following discussions and comparisons I here introduced my evaluation of the ecological groupings of the species.

Free-living (epigean) species. The species are generally widely distributed and winged, and are usually found in mesic forests. To this category also belong the tentative seven undescribed species from Mexico and Guatemala. The species are: *altus, brevior, championi, consobrinus, jamesi, leo, newtoni, oaxaca ulkei.*

Underground nest and burrow (hypogean) species. These live mostly in the soil in the nests and burrows of small mammals, owls, tortoises, and ants. None are host specific. The eyes and pigment may be reduced. All are fully winged. The species are: *californicus, fisus, nevadicus, schwarzi, texanus.*

Edaphophiles. This category includes species inhabiting deep lowland or montane litter and humus. The species have small, pigmented eyes and are wingless. The species are: *meximontanus, shapardi, talamanca.*

Troglophiles (facultative cavernicoles). These species are abundantly known from caves and reproduce there. Their morphology does not suggest that they are cave limited or adapted. They all have large eyes and large wings. This list excludes species that are known from caves but that are judged to be only occasional cave visitors or inhabitants. The troglophiles are: *cavernicola, elabra, spelaeus.*

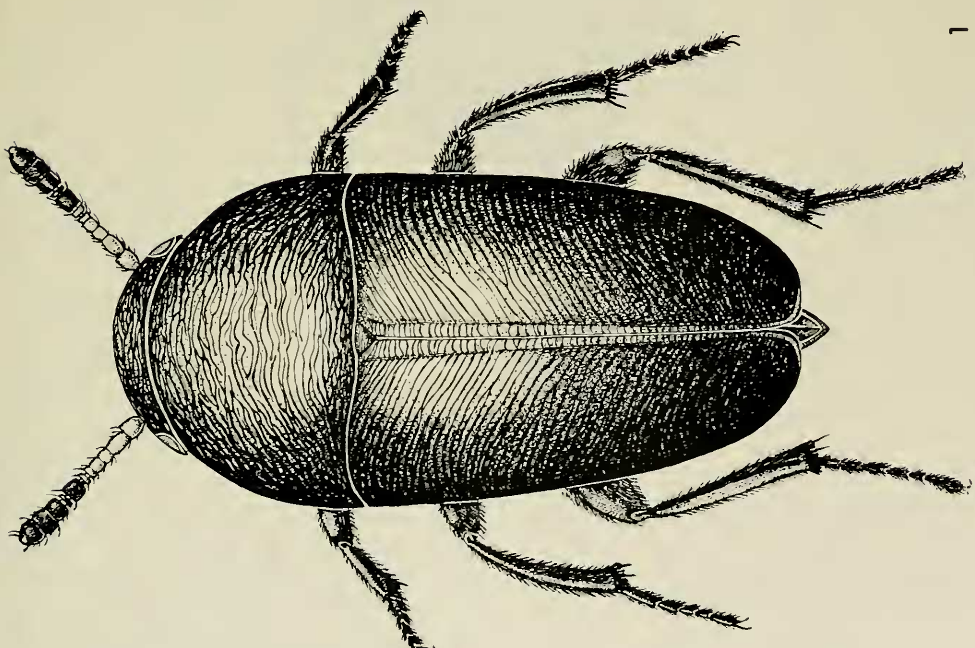
Troglobites (obligate cavernicoles). These species are all known only from caves. They have either small, pigmented eyes, or pale areolae, and all are wingless (or at least with wings reduced to a point judged useless in flight, except in *giaquintoi,* which is fully winged). The species are: *barri, cocytus, episcopus, fiskei, giaquintoi, gypsum, hatchi, hazelae, hirtus, hubrichti, loedingi, nicholasi, troglomexicanus, valentinei, walteri, whiteselli.*

Morphology

Ptomaphagus is mostly holarctic in distribution. Szymczakowski (1964: 60) notes that across this great geographic range the genus presents to the eye a striking monotony. This monotony exists in spite of the considerable number of species. After my following revision of the North American species in the subgenus *Adelops* I find this monotony still to be strikingly present. There has been little development of external morphological differences between the species. This at first forced reliance for species recognition upon the male aedeagus. I now believe the characters of the female spermatheca to be even better for species recognition. However, these species differences are far from being as distinct as the characters of the male and female genitalic structures in many other groups of insects.

Adults. The most striking known changes in the *Adelops* are in the adults (Figs. 1–3). These will be considered first, and the larvae secondly. These differences in morphology are all correlated with what I believe are changes in the occupation of adaptive zones. In other words, as populations began to colonize habitats other than the ancestral habitat of forest litter, the populations experienced new selective pressures, and responded to them. The comparative responses to these pressures, in adult morphology, have been most striking in the troglobitic species.

The morphological expression of adapta-



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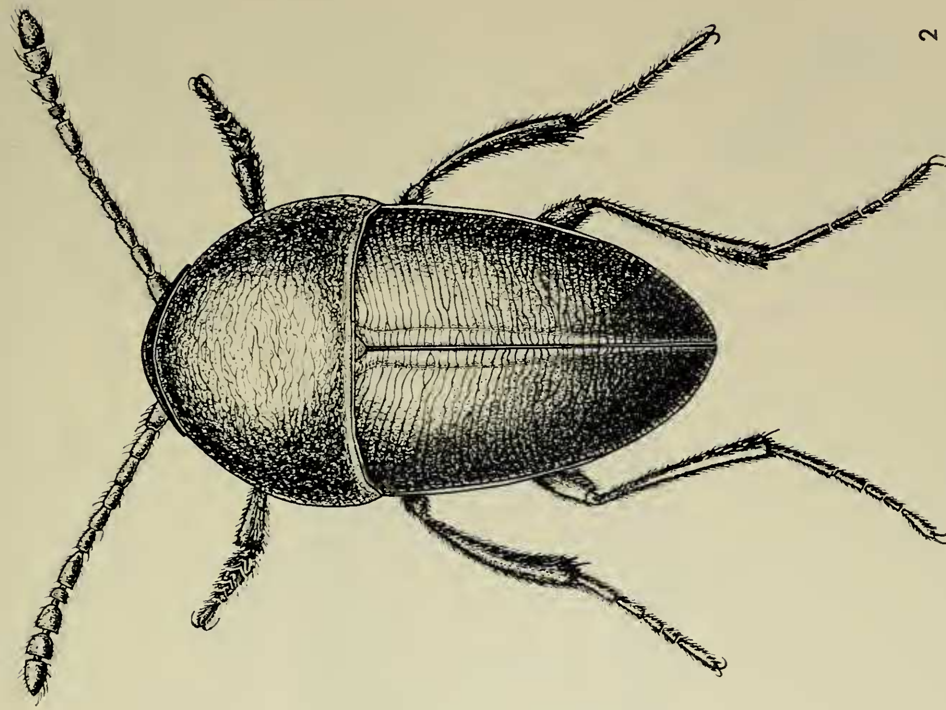

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Figures 1–2. Comparison of general morphology of an epigean and a troglobitic species of *Ptomaphagus*. Fig. 1, *P. consobrinus*. Fig. 2, *P. hirtus*.

tion to subterranean environments is reflected to various degrees in the many species that occupy these habitats. In this category I include not only caves, but cavelike habitats which may offer similar environmental conditions. The *Adelops* of the burrows of animals like pocket gophers display some features very similar to those of species inhabiting caves. Ant nests might also seem to offer cavelike conditions of darkness, a high humidity, and perhaps coolness.

The changes of morphology that have followed the occupation of caves and cavelike habitats can be grouped into two categories. The first category, that of regressive changes, may not be influenced by direct selective pressures for the maintenance of ancestral characters of the population. The character regression may be due to relaxed selection. An alternative explanation is that selection is actively working to remove characters that are no longer advantageous, and may actually be disadvantageous in the cave environment. Under such regressive changes are discussed the reduction of eyes, wings, and pigment. The second category of change, that of progressive changes, seems likely to be a response to active selection. This is most probably the cause of the uniform tendency for elongation of the legs and antennae in the troglobites.

Regressive changes. Numerous explanations have been proposed for the regressive changes in eyes and pigment in cave inhabitants. I will not review these because this has been very well done by Barr (1968). His conclusion is that regressive evolution may be the possible effect of two theories: 1) material compensation (or the economy of developmental energy), or 2) the indirect effect of pleiotropy (combining the effects of pleiotropy, polygeny, mutation pressure, sampling error, limited genetic potential, reduction of variability, and selection). He favors the second alternative.

Eyes. It is possible to construct a sequence of species of *Adelops* exhibiting eye reduction (Figs. 4–6). Such a sequence should be based upon comparing a changing feature of the eyes, such as their horizontal diameter, with a feature that should not be expected to change, such as the lateral width of the head. This has been done in a limited way by Peck (1968) in four species of *Adelops.* Ratios of eye width to head width regress from 0.67 to 0.29 from the largest eyes of *P. brevior* (incorrectly called *consobrinus* in Peck, 1968) to the smallest eyes in *P. loedingi loedingi.*

The ancestral condition of the eye is large, as is seen in Figure 4. This is correlated to forest-litter habitats, and the species generally have wide ranges. In the oldest surviving species group (*hirtus* group), the large-eyed condition no longer exists. An intermediately reduced eye is found in the *hirtus*-group species *shapardi* (Fig. 5), which is a soil and deep-litter inhabitant of the Ozark region. From an ancestor of this sort the remaining *hirtus*-group species (all troglobitic) have probably descended. All these have the eyes reduced to a pale (unpigmented), indistinctly faceted areola (Fig. 6). No *Ptomaphagus* is without at least an eye vestige.

Eye reduction is present but not great in animal-burrow inhabitants of the *consobrinus* group such as *nevadicus, fisus,* and *schwarzi.* In this group, reduction is greatest in the cave-inhabiting *cocytus* and *giaquintoi*, but here the eye width still occupies about half of the head width. In the *cavernicola* group eye reduction is not evident in the cave-inhabitating species *elabra.* All populations of *cavernicola* except that in Cueva de la Boca show little or no eye reduction. Eye reduction in the troglobites *gypsum* and *troglomexicanus* is great, but not as great as in the troglobites of the *hirtus* group. The montane species *altus* (*cavernicola* group), *talamanca* and *meximontanus* (neither assigned to a species group) show marked eye reduction.

In addition to eye size, there is a change

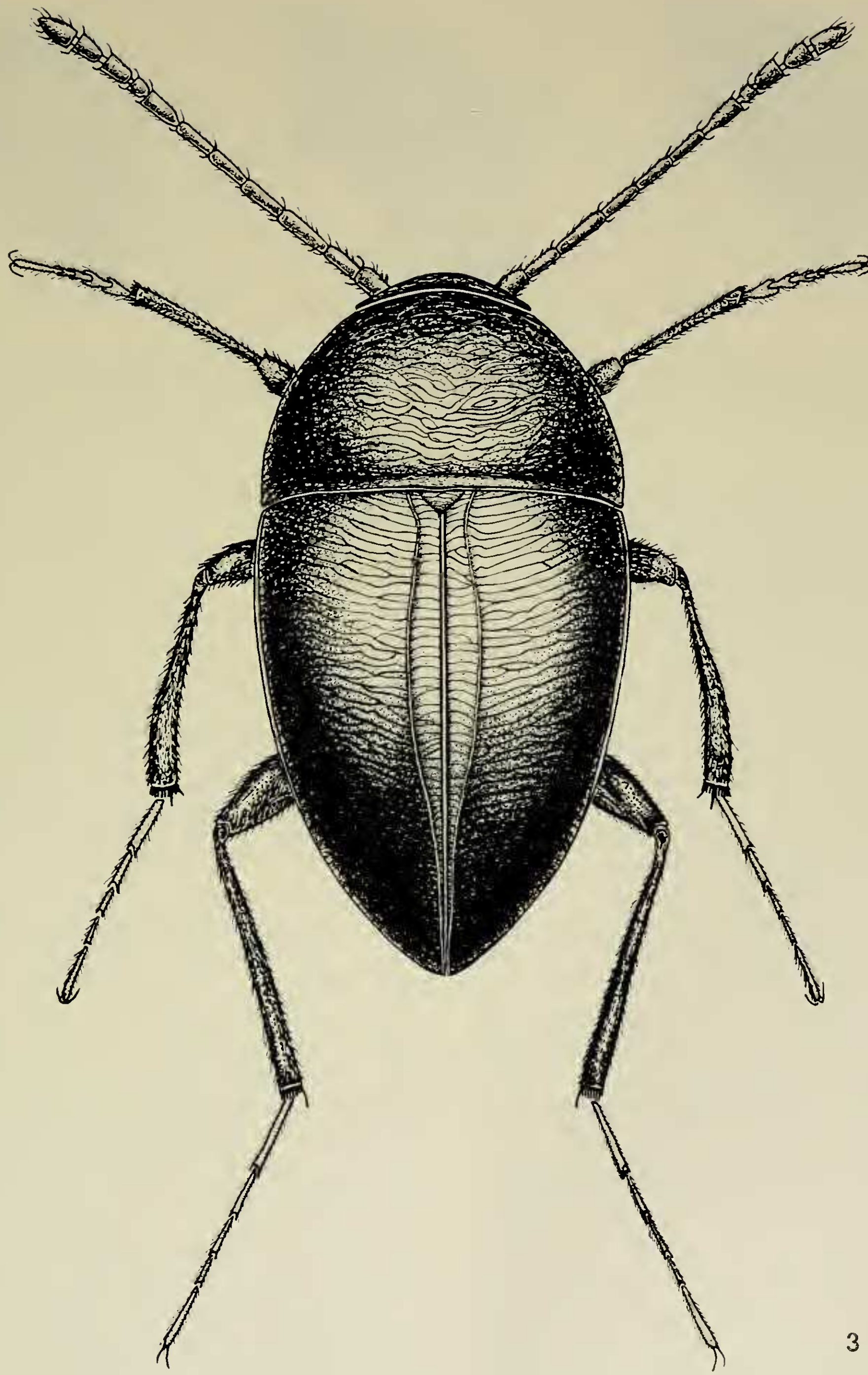

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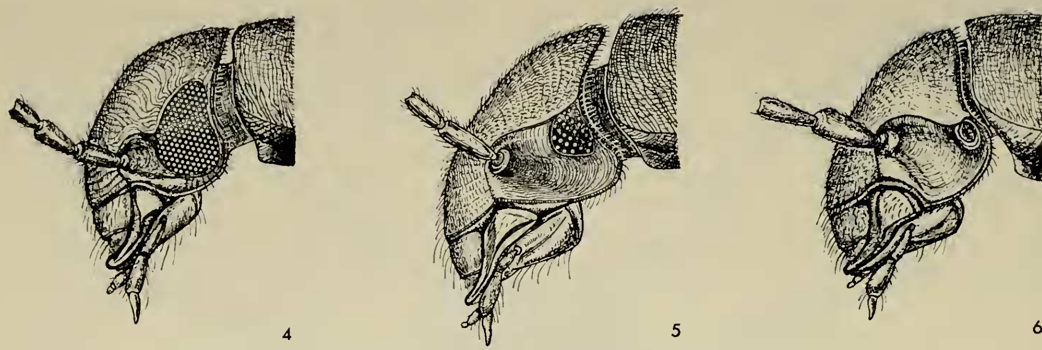
Figure 3. Highly modified troglobitic species, *P. loedingi longicornis*. Compare with Fig. 2, both drawn to same scale.



Figures 4–6. Comparative series demonstrating correlation of eye reduction and habitat restriction. Fig. 4, *P. consobrinus*, wide ranging, epigean. Fig. 5, *P. shapardi*, range in western Ozarks, edaphophilic. Fig. 6, *P. hirtus*, Mammoth Cave region of Kentucky, troglobite. All drawn to same scale.

in the possession of eye pigment. In all cases of eye reduction, only the troglobites of the *hirtus* group, and *gypsum* and *troglomexicanus* have lost the eye pigmentation. The pigmentation is present in the troglobites *cocytus* and *giaquintoi*. Obviously a need exists for the retention of eye pigment in the soil and animal-burrow species so that they can detect light, and avoid it. This need for retention of the optic pigment has obviously decreased for the troglobites.

In the troglobitic *Ptomaphagus* the eyes have not been fully lost. None of them is, strictly speaking, eyeless. However, those that have none of the optic pigment necessary for insect vision can certainly be called blind. Blindness will also result with neural degeneration of the optic tract. The head of the troglobite *P. hirtus* of Mammoth Cave was examined by Packard (1888: 116) and no optic ganglia or optic nerves were found. This lack of neural connection between the brain and the eye rudiment can be assumed for the other troglobitic species of the southeastern United States.

As indicated, all the troglobitic *Adelops* possess eye rudiments. This contrasts strongly with the bathysciines, with the great majority of the 581 Eurasian species being completely anophthalmic. This is a rule in western Europe, but a few eastern European species possess eye vestiges or rudiments. The least reduced of all bathysciine eyes is found in *Adelopsella bosnica*, which is comparable in body size to *P. hirtus*. There are about ten pigmented facets in the eye. The size of these eyes, the least reduced in all the bathysciines, is that of the most reduced *Adelops* eyes.

The American troglobitic trechines also exhibit more eye loss than does *Adelops*. In six trechine genera and about 175 species eye vestiges are completely absent, except in seven species of *Pseudanophthalmus*.

Wings. The loss of wings in beetles is not a phenomenon limited to caves. It occurs in many habitats. Darlington (1936, 1943, 1970) has reviewed and examined some situations selecting for wing reduction in carabid beetles in temperate and tropical, continental and island environments. In many cases in carabids wing dimorphism is present, exhibited as long-winged individuals capable of flight, and short-winged individuals incapable of flight.

In *Adelops*, wing dimorphism within a species is not known. Every individual examined has wings similar to those of the other members of the population and the species. There are three categories of wing condition under which the *Adelops* may be grouped: 1) Fully winged species, which

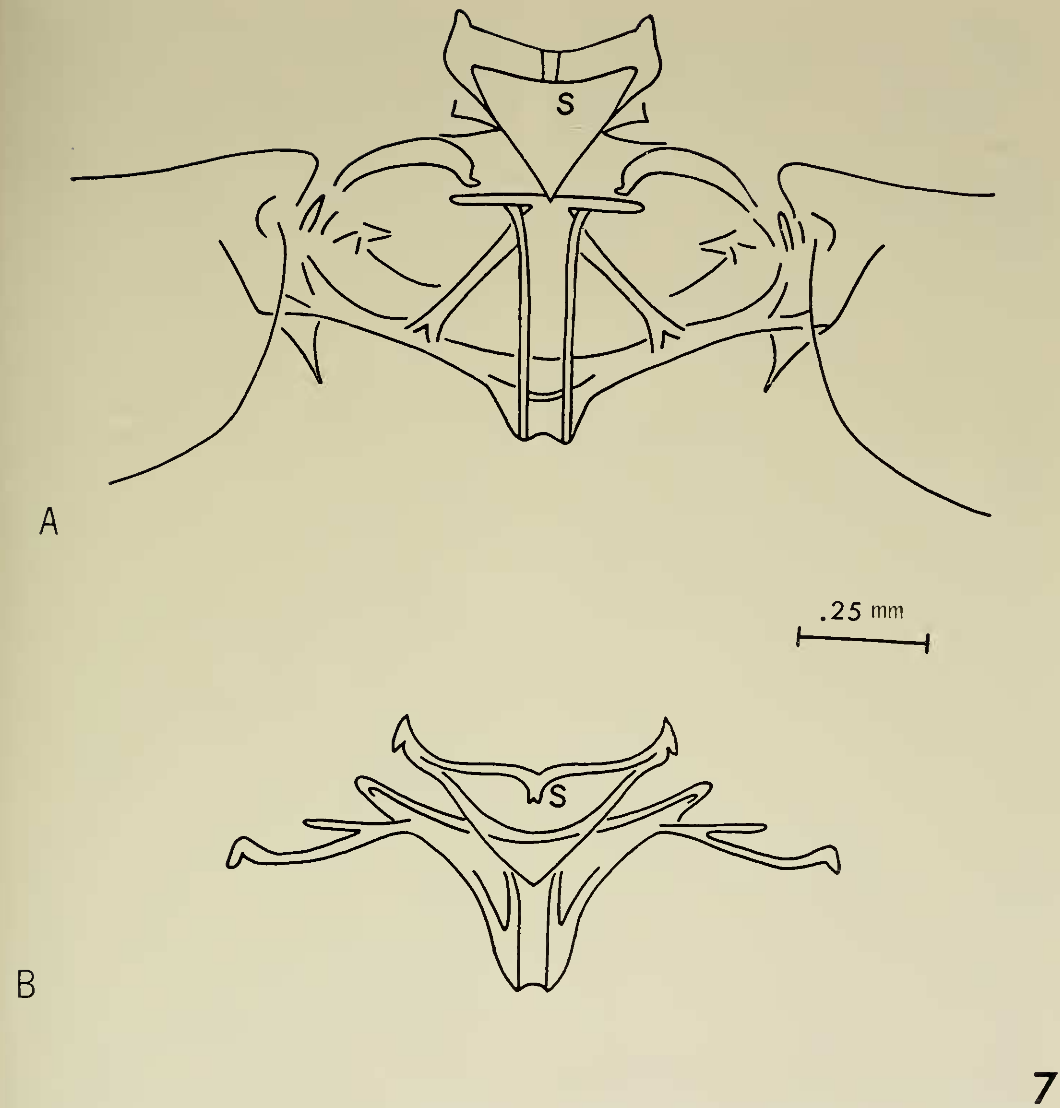


Figure 7. Meso- and metathoracic tergites in *Ptomaphagus*, showing large condition in winged species (A, *P. consobrinus*) and their reduction in a cave-inhabiting species which has wings reduced to a tiny scale (B, *P. hirtus*).

are "free living" and occupy most epigean habitats, as well as the troglophiles, and the troglobite *giaquintoi*; 2) short-winged species, represented by the troglobites *cocytus* and *gypsum* with wings 3/4 the length of the elytra; and 3) wingless species, possessing only a scalelike wing rudiment, containing the edaphophilic and the remaining troglobitic species.

In addition to loss of wings, meso- and metathoracic changes occur. The changes are due to the loss of flight muscles, and the reduction of sclerotized thoracic surfaces serving as attachment surfaces for these muscles. Figure 7 illustrates the comparative reduction in sclerotized regions of meso- and metathoracic tergites in a winged epigean, and a wingless troglo-

bitic species. Darlington (1970) mentions that metasternum reduction accompanies flightlessness in carabids. This is true also in *Ptomaphagus*, although the generalization was tested only on a small sample of specimens of only two species. In *cavernicola* (winged) the ratio of the metasternal length to width is 1:1.8, and in *troglomexicanus* (a wingless derivative from *cavernicola*) the ratio is 1:2.6. Clearly, in this pair of species, flightlessness is accompanied by a reduction in relative metathoracic length.

Pigmentation. The loss of pigmentation in cave animals is most striking in vertebrates and crustaceans that appear white. Cave beetles never become entirely colorless because of a cuticular darkening that accompanies cuticular sclerotization. However, this darkening is less in the troglobitic beetles, probably because of decreased sclerotization accompanying the reduction or loss of actual pigmentation. The epigean species of *Adelops* are darker than the hypogean species. The burrow inhabitants such as *schwarzi* and *texanus*, and the edaphophile *shapardi* are as light as the *hirtus* group troglobites, and *giaquintoi* and *cocytus*. Pigment reduction is only slight in the troglophiles *cavernicola* and *elabra*.

Progressive changes. Comparatively few groups of animals have been able to adjust successfully to the transition from life above ground to life in caves. The many that have show adjustments in morphology and other qualities that preceded cave occupation. Such changes that are adaptive for certain epigean habitats can also be adaptive for cave habitats, and are referred to as "preadaptive." Successful cave colonizations have occurred in North America only in beetle groups already living in cool, dark, moist habitats, quite often at higher montane elevations. Probably the strongest preadaptations are behavioral and physiological.

The events of preadaptation, colonization, and adaptation are presented by Barr (1968), and will be considered for *Adelops* in the discussion of evolution. Once cave occupation was achieved, different sets of selective pressures operated upon the populations. The most striking progressive adaptation in troglobitic beetles is the tendency for elongation of the appendages (seen clearly in Figs. 1–3). However, their selective advantage is not clear (Barr, 1968). Perhaps elongation of appendages provides more surface area to be covered by sensory hairs. Perhaps leg elongation allows the beetles greater searching ability in food-poor caves. But if there are advantages in having longer appendages, why have they not also appeared in the epigean Trechini, Ptomaphagini, and Pselaphidae? It is probably because the epigean species dwell in habitats constricted by rocks, roots, moss, and debris where the longer appendages would be a hindrance rather than a help. The epigean species must remain in these constricted habitats for the conservation of moisture, and the avoidance of heat, light, and predators. With the ancestral entry into caves, the predation pressures were lessened because the predator species diversity and density in caves was less than in epigean situations. The suitable darkness, coolness, and the moistness of caves allowed an ecological release which opened the possibilities of foraging on the surface of the cave soil substrate rather than under the surface (such as in epigean soil, litter, and moss). In fact, the caves presented very few opportunities for subsurface foraging compared with epigean environments. Hence, one of the requirements for successful cave occupation was the ability of the colonizer to act as a surface forager. From the substrate surface occupation in caves came release from the selective factors that had kept appendages short in epigean subsurface species.

Mesosternal carina. I do not know of any previous works that have considered this structure in relation to cave adaptation. In *Adelops* I have noticed that its

degree of development is strongly related to the general degree of cave specialization of the species, and thus it is a progressive structure (Figs. 78–97). In the *hirtus* group it is low in *shapardi,* and of medium-to-high development in the troglobitic species. In the *consobrinus* group the carina is stronger in the troglobite *cocytus* than in *fisus,* the ancestral form. All other species in the group have a low-to-medium carina except for the well-developed carina of *giaquintoi,* a troglobite from Guatemala. In a close-knit cluster of species in the *cavernicola* group, the carina is least developed in the forest-inhabiting *oaxaca,* more developed in *cavernicola,* and most developed in *troglomexicanus,* although in the latter the carina is not as prominent as in the other species-group troglobites.

It is useful to test the idea that the carina is a cave-dependent feature by examining the Bathysciini. The following generalizations are only suggestions because of the limited number of genera (21) and species (38) that I have examined. The carina is low in *Platycholeus* inquilines. In the Bathysciina (Bathysciini of Laneyrie, 1967) the humicoles *Adelopsella* (which has the largest eyes of the subtribe as noted above) and *Sciaphyes* have a low carina. All of the following considered species and genera are troglobites in the list of Lanyrie (1967). For the most simple analysis they will be considered only with regard to their ecology, body shape (defined later), and carina size and not to their phyletic relationship. Of species (within a genus there is variation in carina size) with a bathyscioid body shape, two have a low carina, four have a medium carina, and 18 species (in five genera, 14 species in *Speonomus*) have a high carina. Of those with a pholeuonoid body shape five species (in four genera) have a low carina and two species (in two genera) have a medium carina. Of those with a leptodiroid body shape, one species has no carina, and another has a very low carina. In the Antroherponina (with six genera), which are all troglobites of the leptodiroid (or scaphoid) body form, the carina is present but very low in *Spelaeobates* and absent in *Antroherpon* and *Remyella.*

I interpret the above observations of Bathysciini as suggesting that the carina is a progressive and cave-dependent structure in the early stages of cave specialization and evolution, defined and characterized by the bathyscioid body shape. This is also true in *Adelops,* which also has this body shape. With further evolution and gradual acquisition of the pholeuonoid body shape the carina partly or completely loses what must be a functional significance. The reduction and loss of the carina occurs as the species acquire the very modified leptodiroid body shape in both the subtribes Bathysciina and Antroherponina. Here the carina is very low at most.

Discovery of the functional significance of the carina may come from careful studies of comparative behavior, combined with functional morphology. The answer probably lies in a combination of factors involving digging, walking, burrowing, and hiding.

Appendages. Figure 8 is a series of antennae demonstrating the length-to-width proportions of species of different species groups, ecologies, and levels of adaptation. Figures 15 and 16 demonstrate the comparatively more slender femur of *cocytus,* and its probable ancestor *fisus.* A preliminary documentation with measurements of antennal and leg elongation was presented by Peck (1968). The troglobitic *Adelops,* unlike agonine carabids and some pselaphid beetles do not demonstrate an elongation of maxillary palps.

In comparison to *Adelops* an interesting summary of the morphological trends of the preadaptation and adaptation of the Bathysciini is that of Vandel (1965: 204). He views the process, summarized below, as conclusive "orthogenetic evolution." I do not, because I believe the direction is determined by natural selection, which is excluded in orthogenesis (Mayr, 1963).

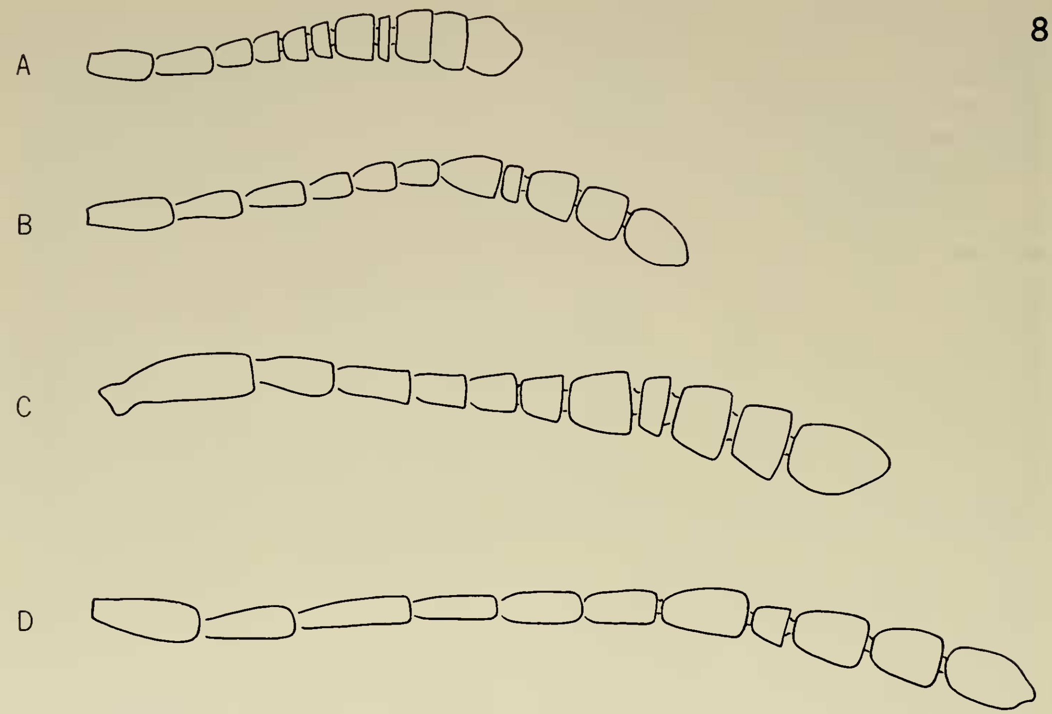


Figure 8. Progressive elongation of antennae in *Ptomaphagus*. The increased length is partially due to an allometric increase in body size, but is more closely related to overall degree of cave adaptation of the species. A, *P. consobrinus*, epigean. B, *P. hirtus*, troglobite. C, *P. cavernicola*, troglophile. D, *P. loedingi longicornis*, troglobite. All to same scale.

The bathysciines were preeminently preadapted for cave life. All of the surviving noncave species possess characters associated with cave life. The early evolution was probably associated with montane forests, during which they became depigmented, wingless, and eyeless (or at least microphthalmic). The early stages of cave colonization were accomplished by preadapted forms similar to the Mediterranean moss-inhabiting genus *Bathysciola*. Cave evolution proceeded independently in two directions in Mediterranean Europe owing to a seaway separating the western Tyrrhenian form the eastern Aegean stocks of Bathysciini. A large number of endogean (edaphobitic) and little-specialized cavernicoles are found today, having an ovoid body and short appendages. Such "bathyscioid" types are *Speonomus* (Pyrenees), *Diaprysus* (Cevennes), *Cytodromus* and *Royerella* (Alps) in western Europe, and *Aphaobius, Bathysciotes,* and *Neobathyscia* in eastern Europe.

In the final stages of evolution, not only the appendages, but also the body became more elongate. Body elongation is not noticeable in *Adelops*. This "pholeuonoid" type of bathysciine also has a thinner pronotum with indistinct or obliterated margins. Such specialized cavernicoles are *Antrocharis* and *Isereus* of western Europe and *Pholeuon* and *Apholeuonus* of eastern Europe. These specialized types sometimes live in extraordinary habitats such as ice caves. For instance *Isereus xambeui* has been found in a French cave with temperatures of 0–1°C, and *Pholeuon glaciale* inhabits an ice hole in Transylvania with summer temperatures rarely exceeding 0.8°C.

Ultra-evolved forms are called the "lepto-

diroid" type. These are few, and are limited to the Yugoslavian region. The legs and antennae are extremely long, the head and prothorax are narrow and elongate, and the elytra have a tendency to widen. This last results in a spherical abdomen in *Leptodirus*.

A remarkable cave convergence exists between the "leptodiroid" form and a recently described beetle from lava tube caves in Idaho. The Idaho *Glacicavicola bathyscioides* Westcott (Leiodidae; Glacicavicolinae) has a strong external resemblance to the leptodiroid genera *Astagobius* and *Antroherpon*. Its existence in caves in contact with ice recalls the above mentioned pholeuonids, although *Glacicavicola* is seemingly not dependent upon freezing temperatures (Peck, 1969).

Larvae. Except for what will be reported in a later paper on life cycles, I have paid very little attention to *Adelops* larvae. The larvae of only a few epigean species are known to me from only a few specimens. In contrast, through collections and cultures, many larvae are available of several troglobitic species. Although I have not closely compared the larvae of epigean and troglobitic species, in brief examination I have seen that there is only one striking difference between them.

This difference, which may be categorized as regressive, is that in the *hirtus* group troglobites, the larvae have entirely lost the eye spot. No other comparative differences are present.

Larvae of only two species of *Ptomaphagus* have been described and illustrated in the literature: the epigean *P. sericatus* from Spain (Jeannel, 1922: 50) and the troglobitic *P. hirtus* from Kentucky (Jeannel, 1931: 409; Böving and Craighead, 1933: 109). When these larvae from different habitats and different continents are compared no differences are evident except in the eyes.

The larval uniformity of *Ptomaphagus* is, again, in striking contrast to the larval differences of the bathysciines. Deleurance-Glaçon found many regressive changes in larval morphology associated with life-cycle modifications. These modifications are all a response to a decrease in importance of the larval stage in the life cycle.

The classic (nonevolved) larval type, consisting of two or three instars of larvae that feed, was found to be characterized by the following morphological points (Deleurance-Glaçon, 1963a: 71):

1. All large dorsal cranial, thoracic, and abdominal hairs composite.
2. Body normal, not fat with food reserves.
3. Mandibles dissymetrical.
4. Mola with retinaculum and prostheca.
5. Molar teeth numerous, important.
6. Galea with wide thick fringe of setae.
7. Paraglossae visible on dorsal labial face.
8. Cerci long, biarticulated, second article long and ciliated.

The evolved larvae, of only one nonfeeding instar which corresponds to instar I of the classic type, differs in (Deleurance-Glaçon, 1963a: 84):

1. All large dorsal cranial, thoracic, and abdominal hairs single.
2. Body thick, fat with food reserves.
3. Mandibles symmetrical.
4. Mola lacking retinaculum and prostheca.
5. Molar teeth few and small.
6. Galea fringe short and reduced.
7. No paraglossae.
8. Cerci short, uniarticulate.

It can readily be seen that the differences in the evolved larvae are ones involving a decrease or reduction in feeding and sensory structures. The specialized morphology parallels a specialized life cycle.

Anatomy and Histology

The only anatomical and histological work with *Ptomaphagus* is the previously mentioned study of the head of *P. hirtus*

(Packard, 1888: 116), in which it was found that there were no traces of optic nerves or optic ganglia.

The great morphological and life-cycle changes observed in the Bathysciini led Deleurance-Glaçon (1963a) to compare internal characteristics of the beetles. I have not done this with *Adelops* because of the slight prospect of encountering differences. In comparisons of the female reproductive tract, she found that both classic and evolved species have a pair of ovaries, each with five to six ovarioles. There are many active ovarioles in the species that produce small eggs. In the species that produce large eggs, only one ovariole acts at a time in maturing an egg. The ovarioles are acrotrophic (= telotrophic). No major histological differences exist between the ovaries of large and little egg species. The only differences are physiological ones (concerning vitelogenesis), in variation in trophocytes and follicular cells. Oogonia divisions occur in the pupa, beginning in the fourth month of larval life, with no divisions in old pupae or adults of oocytes or trophic tissues.

The ovariole invariability contrasts with findings (Deleurance-Glaçon, 1963b: 234) in a series of troglobitic trechine beetles in which the ovariole number decreases from six per ovary down to one (in five species of *Aphaenops*). This may be connected with the fact that carabid ovarioles are polytrophic.

The bathysciine digestive tract also shows modification between the classic and evolved types. In classic larvae the digestive tract is similar to that of other coleoptera. The mid-gut is large, with a well-developed cavity. The hind-gut is folded upon itself. There are four short and fine Malpighian tubules. In the evolved larvae, the digestive tract is nonfunctional. The mid-gut is small and closed. The hind-gut is straight, nonfunctional and very slender. The four Malpighian tubules, entwining the hindgut, are greatly increased in size and length, with a very narrow lumen. However, the digestive tract of embryos of the evolved species is functional and similar to that of the classic larvae.

Behavior

Most observed insect behavior is associated with reproduction. This is especially true for *Adelops* because, other than in reproduction, they have little or no behavior at all. All the *Adelops* observations reported below were of laboratory cultures of beetles at natural cave temperatures and humidities. The techniques used for culturing the beetles will be discussed in a later paper.

Adults. The beetles are most often observed as motionless. I have not attempted to determine if there is a circadian or other rhythm of activity. Epigean and cave species display a desire to be under soil particles. This is more pronounced in the epigean and troglophilic species. Upon being disturbed the troglobitic species are more inclined to run about than the epigean species.

Nothing differs in feeding behavior between the epigean and troglobitic species except that the epigean species (*brevior*) feed well on human dung but not on wet yeast, which the troglobitic species eat.

There is no courtship behavior. Males will instantly mount females and copulate. I have never seen what appeared to me to be a female rejecting a male. Copulation seldom lasts more than thirty seconds. During copulation the male may antennate the female. I do not know about the other species, but in the troglobites there is no copulatory seasonality or cycle.

During copulation *hirtus* females behave differently than the females of other observed species. Female *hirtus* flex downward at the pronotal-elytral junction, thus elevating the abdominal tip toward the male. The female does not flex in the other species.

All species coat their eggs with small soil

particles and debris. This is done by the female at the time that the egg is being extruded from her body. As she extrudes the egg she searches the area around her with her antennae and mouthparts. The soil and debris particles are gathered by the palps and mandibles. As observed in troglobitic species, the female then rears back on her meso- and metathoracic legs, takes the soil particles from the mouthparts with her protarsi and carries them to the egg. The soil is patted onto the egg with both protarsi. This process was observed for up to eight minutes in a female *loedingi longicornis* from Paint Rock Cave.

Data on age at sexual maturity, egg-laying frequency, sperm storage ability and so forth will be given in a later paper. Males and females may remain reproductively competent until their death. This is true for two male *hirtus* at 12.5°C which fathered larvae three years after their capture as adults. There is no obvious egg-laying cycle.

In comparison, Deleurance-Glaçon (1963a) found in the bathysciines that there is no circadian rhythm but that females are more active than the males. In activity, *Speonomus* type (classic) beetles are agile, while *Leptodirus* type (evolved) beetles are slow and clumsy. Activity is a regular variation of rest and activity at temperatures ranging from 0°C–20°C. Lethal points are –5°C and +25°C. There is no feeding cycle in the males, but the females feed according to their egg-laying cycle. There is no precopulatory behavior. Copulation is throughout the year, with no refractory period, lasts less than half an hour, and may be accompanied by antennal caressing. Virgins lay infertile eggs irregularly and infrequently. Sperm storage in the females may be as long as 13 months. Sexual maturity is reached three to five months after eclosion. Sexual competency may last through the adult life span of four to five years. Females may lay up to 500 eggs in four years in species with unmodified life cycles (291 actually observed in *Speonomus delarouzeei*) and 60 eggs in four years in species with contracted life cycles (31 actually observed in *Troglodromus bucheti*). There is no seasonal egg-laying cycle. There is a periodicity of egg-laying at about every 25 days in *Isereus serullazi*. The species with the classic (unmodified) life cycle show no periodicity and produce a dozen or more eggs a month. The percent of individuals that are fertile varies from 42 percent to 93 percent and is species dependent.

Larvae. Mature larvae of *cavernicola* show a very strong tendency to climb to the top of the culture box. This may be a reflection of searching for "high ground" for pupation, which may have adaptive significance in lessening the chances of pupal death by flooding. Mature larvae of other species crawled to the top of the culture boxes but never in such large proportions.

Mud cells are made by the larvae only for pupation, never for inter-instar moulting as in the Bathysciinae. A marked difference in cell construction exists between the nontroglobitic and troglobitic species. Both *brevior* and *cavernicola* larvae dig straight down into the clay substrate, pushing the dirt crumbs above them and forming a cell whose top is 2–3 mm under the substrate. Seemingly, predation or other pressures are relaxed in the troglobites because they form a more exposed and vulnerable pupation cell. Their cell is a thin-walled mud igloo rising as a small dome above the substrate. These cells appear not to be strong enough to resist predation of the pupae by cave carabids or crickets. These cells are probably sufficient protection against mites and collembola, which I have seen feed on exposed *Adelops* pupae.

SYSTEMATIC POSITION OF *PTOMAPHAGUS*

Introductory comments are necessary concerning the higher categories contain-

ing *Ptomaphagus*. These comments are needed because of the various systems of classification employed in various museums and by various workers in the Old and New Worlds. There is comparative uniformity only on placement of the higher taxa within the superfamily Staphylinoidea. On the family level, the literature of the early 1900's and before placed *Ptomaphagus* in the family Silphidae and usually in the subfamily Catopinae. This is still the case in the *Zoological Record*.

Hatch (1933) reviewed the group for the United States and separated it as a family unit from the Silphidae, a procedure which has been generally followed ever since, and employed the name Leptodiridae. Jeannel (1936) monographed the unit as the family Catopidae, and this usage has strongly influenced continental Europeans ever since.

Within the Staphylinoidea I prefer the conservative, and I believe evolutionarily sound, family classification systems of Hatch (1957) and Crowson (1967). Here the family unit is Leiodidae (=Anisotomidae), containing the subfamilies Catopinae, Leiodinae (=Anisotominae), Catopocerinae, Coloninae, Camiarinae, Scotocryptinae, and Glacicavicolinae. The last was proposed by Westcott (1968).

Family LEIODIDAE

Staphylinoidea with 11-segmented antennae; 5-segmented club; long elytra covering abdomen except for posterior 1 or 2 tergites; front coxal cavities closed behind (except Leiodinae–*Hydnobius*); male almost always with dilated protarsi, hind coxae usually contiguous upon removal of coxae; front coxae transverse or conically projecting. Larvae with mandible with prostheca or retinaculum and mola; maxillae with apex of stipes simple, galea not articulated.

I prefer the family name Leiodidae over Anisotomidae simply because I think it is more widely recognized by coleopterists.

A world study of the subfamily Catopinae was first undertaken by Jeannel (1936). Szymczakowski (1964, 1969a) revised the tribal ranking. I have taken these works and generally lowered the category by a unit to the higher categories that follow because I believe that the taxonomic fragmentation begun by Jeannel is impractical. In the "lumping" system that I follow, the evolutionary relationships are, I believe, better demonstrated. This is a desire on my part to avoid inflating the value of the higher categories. Certainly Jeannel and Szymczakowski contributed many valuable suggestions from their greater breadth of study of the Catopinae and I have tried to pay due consideration to them in the taxonomic arrangement here proposed.

Subfamily CATOPINAE

Characterization. Leiodidae with loose antennal club, segment 8 always smaller than 7 or 9; head with occiput raised posteriorly into a keel which overlies front margin of pronotum (except in Nemadini–Argytodina living only in New Zealand, Australia, and southern South America); front coxal trochantins hidden. Larvae with doubly fringed maxillary galea, urogomphi long, slender, often multi-articulate.

Coordinate taxa. Leiodinae (=Anisotominae), Camiarinae, Scotocryptinae, Coloninae, Catopocerinae, Glacicavicolinae.

The following key, modified from Jeannel (1936), will serve to separate the tribes of Catopinae. Explanatory illustrations may be found in Jeannel. The key is based on male genital characters, which are the least ambiguous characters available, and serve the second function of reflecting relationship and phylogeny.

Key to Tribes of Catopinae

1a. Posterior coxae separated, female with 4 protarsal segments, male with 5 or 4 .... *Bathysciini*

1b. Posterior coxae contiguous, male and female with 5 protarsal segments 2

2a. Male copulatory organ with complete tegmen, parameres not inserted directly on aedeagus 3
2b. Male copulatory organ without tegmen, parameres inserted directly onto aedeagus 5
3a. Genital segment reduced to a chitinous ring around base of aedeagus .... *Catopini*
3b. Genital segment tubular, not reduced 4
4a. Ventral blade of tegmen full and flattened. Epistome indistinct. Next to last maxillary palp segment not swollen. Male mesotarsomeres narrow, or only first segment dilated .... *Nemadini*
4b. Ventral blade of tegmen reduced to narrow transverse chitinous band. Epistome separated at front. Next to last segment of maxillary palp ovoid and swollen, last segment very small. Male with first 2 mesotarsomeres dilated .... *Anemadini*
5a. Aedeagus short, triangular, flat, wide at base; basal blade large and free; last article of maxillary palp long and fusiform .... *Eucatopini*
5b. Aedeagus elongate, oval, narrow at base; basal blade reduced; last article of maxillary palp short and conical .... *Ptomaphagini*

Tribe PTOMAPHAGINI

Ptomaphagus phyletic series, Jeannel, 1922: 41.
Ptomaphagini, Jeannel, 1936: 52.
Ptomaphaginae, Szymczakowski, 1964: 58.

Description of tribe. Form oval, elongate (except in the myrmecophiles *Synaulus* and *Echinocoleus*). Prothorax transversely striate (except in some cave *Ptomaphagus*, and in *Pandania*). Last article of maxillary palps conical, a little longer than preceding segment. Pronotum transverse, widest at base, or up to 1/3 from base. Mesocoxae separated, mesosternum carinate on midline. Mesepimeron and mesepisternum distinct, separated by a suture. Metepisternum wide, triangular or trapezoidal. Metacoxae contiguous. All tarsi pentamerous in both sexes. Summits of all tibiae armed with comb of short equal spines. Genital segment reduced, not tubular, reduced to flattened pleurosternite. Tegmen of male copulatory organ lacking a ventral blade; parameres inserted at base of aedeagus not united by a ventral ring. Aedeagus elongate, sometimes highly modified but never having the form of two triangular valves as in Eucatopini (=Eucatopini *sensu* Jeannel, 1936). Aedeagus basal blade atrophied. Parameres more or less fused to aedeagus. Internal sac of ejaculatory duct armed with long evaginable stylet, but without accessory sclerotized pieces. Aedeagal orifice ventral in primitive species of *Adelopsis, Ptomaphaginus,* and *Proptomaphaginus,* but in most species it has passed to the dorsal surface, cutting the right margin (subtribe Ptomaphaginina) or the left margin (subtribe Ptomaphagina); this displacement produces an asymmetry, sometimes very great (in certain *Adelopsis*).

Coordinate taxa: the subfamilies of Szymczakowski (1964: 59) lowered to tribal status: Eucatopini, Nemadini, Anemadini, Catopini and Bathysciini.

The tribe is distributed throughout much of the New World, and the Palearctic and Oriental Regions. It does not occur in sub-Saharan Africa, or in the Australian Region. It can be easily divided into two major evolutionary lines, here treated as subtribes.

Key to subtribes of Ptomaphagini

1a. Anterior tibiae with distinct comb of short spines on outer margin, as well as apex (Fig. 11). Mesepisternum transverse, as wide at inner edge as at outer edge (Fig. 9) .... *Ptomaphaginina*
1b. Anterior tibiae with comb of short spines only on apex (Fig. 14). Mesepisternum trapezoidal, wider on outer edge than inner edge (Fig. 10) .... *Ptomaphagina*

Subtribe PTOMAPHAGININA

Ptomaphaginini Szymczakowski, 1964, 1969a.

Characterization. Mesothoracic epimeron small and very transverse (Fig. 9), twice as wide as long, its internal border subequal to external border. Anterior tibiae with comb of short equal spines on apex and outer margin. Migration of aedeagal orifice to dorsal surface by way of right side.

The group contains three genera: *Pro-*

ptomaphaginus, *Ptomaphaginus*, and *Pandania*.

KEY TO GENERA OF PTOMAPHAGININA

1a. Male and female protarsi similar (Figs. 11, 12). West Indies and Mexico .... *Proptomaphaginus*
1b. Male and female protarsi dissimilar, male segments swollen. Oriental Region 2
2a. Pronotum with transverse striae, widest at hind angles of base, mesosternal carina relatively low .... *Ptomaphaginus*
2b. Pronotum without transverse striae, only punctuation; widest before base, mesosternal carina high, leading edge angular .... *Pandania*

Genus *Proptomaphaginus*

Proptomaphaginus Szymczakowski, 1969a: 88. Type species *P. apodemus* Szymczakowski.

Characterization. Sexual dimorphism of protarsi not present, male and female protarsi narrow. This is an exceptional character, because all other nonbathysciine Catopinae have males with widened protarsal segments. Aedeagus symmetrical, with notch in tip. Spermatheca simple crescent-shaped tube.

The genus is reported only from the West Indies, but is known to occur in Mexico. Three species are described: *apodemus* Szymczakowski 1969a from Cuba, *darlingtoni* (Jeannel) 1936 from Cuba, and *puertoricensis* Peck 1970a from Puerto Rico. Szymczakowski (1969a) and Peck (1970a) contain additional discussion of the genus, its ecology, and its zoogeography.

Genus *Ptomaphaginus*

Ptomaphaginus Portevin, 1914: 194. Type species *P. longitarsis* Portevin.

Characterization. Size small, 1.1–3.4 mm. Form oblong, convex. Pubescence short, golden, decumbent. All dorsal surfaces covered with fine transverse striae, oblique on elytra. Winged or wingless, always eyed. Male protarsi wide, female protarsi narrow. Aedeagus broad and short, tip variable in shape, orifice on ventral surface, or cutting right margin of aedeagus in shift to dorsal surface. Spermathecae unknown.

The genus is limited to the Oriental Region. It was revised by Jeannnel (1936) and Szymczakowski (1964) with five species later described (Szymczakowski, 1965, 1970; Henrot and Szymczakowski, 1971). Complete literature citations for the older species are in the first two revisions, and are not given in my list of references. The twenty-six recognized species are listed with their localities or ranges as follows:

angusticornis (Portevin) 1921; Java
bryanti Jeannel 1936; Borneo (Sarawak)
cilipes (Portevin) 1907; southern India
clibanarius Szymczakowski 1970; Singapore
flavicornis (Motschoulsky) 1863; Ceylon
gracilis Schweiger 1956; southern China (Foukien)
honestus Szymczakowski 1964; northern Burma
jacobsoni Szymczakowski 1964; Sumatra
latescens Szymczakowski 1964; Sumatra
lacertosus Szymczakowski 1970; Singapore
laticornis Jeannel 1936; Eastern India (Assam)
latipes (Pic) 1929; Philippines (Mindanao)
lewisi Szymczakowski 1964; Ceylon
longitarsis Portevin 1914; Ceylon
murphyi Szymczakowski 1970; Singapore
nitens Jeannel 1936; Ceylon
obtusus Szymczakowski 1959; Sumatra
oribates Szymczakowski 1965; Nepal
parvulus Henrot and Szymczakowski 1971; Ceylon
portevini Szymczakowski 1964; Sumatra
rubidus (Champion) 1927; northern India
rufus Jeannel 1936; Sumatra, Singapore
sauteri Portevin 1914; Taiwan
scaber Szymczakowski 1964; northern Burma
similis Schweiger 1956; southern China (Foukien)
tantillus Szymczakowski 1964; Malaya, Singapore
tarsalis Szymczakowski 1964; Sumatra

Virtually all of these species are known only from the type collections. Little is reported about their habits or habitats (except in Szymczakowski, 1970). They should all be expected as inhabitants of moist forest litter. *P. cilipes* was found marching in a column of ants, and shows some adaptations for myrmecophily. *P. latescens* and *obtusus* were taken in caves in Sumatra but do not look as if they are cave-limited species.

Genus *Pandania*

Pandania Szymczakowski, 1964: 148. Type species *P. oxytropis* Szymczakowski.

Characterization. Length 2.6 mm. Form ovoid, slightly convex. Pronotum widest before base; lacking striae, only sparsely punctate. Mesosternal carina strongly developed, borders projected, forming right angle.

The genus is known only from the female of the type species from Sumatra.

Subtribe PTOMAPHAGINA

Ptomaphagini Szymczakowski, 1964, 1969a.

Characterization. Mesothoracic epimeron large, about as long as wide, its external border wider than the internal (Fig. 10). Anterior tibiae with a comb of small equal spines limited to the apical edge and not occurring on the external margin (Fig. 14). Migration of the aedeagal orifice to the dorsal surface via the left margin of the aedeagus.

This is a large group occurring in the Holarctic and Neotropical regions. Four genera are contained and can be distinguished in the following key:

Key to genera of Ptomaphagina

1a. Form oval, with long erect hairs as well as short hairs, myrmecophile (southern United States) .... *Echinocoleus*
1b. Form elongate, with short recumbent hairs only 2
2a. Aedeagus broad and short; apex variable; orifice central, or cutting to dorsal surface by left side (Figs. 9, 10) (southern United States to central South America) .. *Adelopsis*
2b. Aedeagus long and thin; orifice always on dorsal surface, always cutting left side 3
3a. Antennae very short, article 3–10 very transverse, legs and tarsi very short, tibiae flattened and quadrangular, myrmecophile (North Africa) .... *Synaulus*
3b. Antennae and legs not shortened (Holarctic and Neotropical regions) *Ptomaphagus*

Genus *Echinocoleus*

Echinocoleus Horn, 1885: 136. Type species *E. setiger*, holotype seen.

Diagnosis. The pale color, wide oval shape, and long erect golden hairs serve to distinguish this genus. It is known only from ant nests in the southern United States from Alabama to Arizona.

Description of genus. Length 2.5–2.8 mm. Width 1.5–1.8 mm. Color pale yellowish or reddish brown. Form oval, 1.9 times as long as wide; flattened. Head smooth, with fine hairs; eyes large. Antennae short, not reaching the middle of pronotum when laid back; all segments except III transverse; last 8 segments increasingly wider so that XI is widest. Pronotum widest at base, twice as wide as long; sides regularly arcuate; hind angles drawn out but rounded; hind margin straight in middle; striae absent on disc or present as minute striolae; covered with recumbent short, or recumbent short and erect long hairs. Elytra widest at base, as long as wide to 1.2 times as wide as long; external apical angles rounded, hind margins rounded-truncate; sutural angles sharp in male and female; striae transverse to suture; dense vestiture of long erect and short recumbent hairs. Wings absent. Mesosternum with very low carina on midline. Mesepimeron of Ptomaphagina type, trapezoidal. Legs short, flattened; comb of short equal spines on summit of all tibiae; protarsi dilated in both sexes, mesotarsi narrow in both sexes. Aedeagus in side view blunt at base, tapering gradually to narrow tip; style of internal sac long, thin, twisted; in dorsal view narrowing gradually toward tip, tip a blunt point; parameres long, thin, lying close to aedeagus. Genital plates twice as long as broad, median spiculum gastrale elongate, projecting 1/2 length beyond anterior end of genital plates. Spermatheca with narrow posterior, large swollen twisted anterior end.

Species. The genus contains only one named species, *setiger* Horn 1885. Jeannel (1936) transferred *Dissochaetus arizonensis* Hatch 1933 into *Echinocoleus*, without having seen material of either species. I

have seen the types of *arizonensis,* and it is a *Dissochaetus,* in the tribe Nemadini. Jeannel (1936) also placed *Echinocoleus* in the Nemadini, which would not have happened if he had seen this very distinctive and highly modified genus of Ptomaphagina.

Ecology and distribution. I have seen material representing three species. Horn reports only two specimens in his series from Arizona. I have seen one taken in March 1919 from Oracle, Arizona, 5000 feet, pinned with *Novomessor albisetosus* ants (F. G. Werner det.), one from Las Vegas, New Mexico, pinned with a *Pogonomyrmex* ant, three taken in April 1970 from a *Pogonomyrmex rugosus* nest in Tucson, Arizona, and one from a *Pogonomyrmex* nest at Selma, Alabama.

One larva was recovered from a *Pogonomyrmex* nest. The larva is modified from the usual elongate shape of Ptomaphagina into a very broad and flat form with abundant large and thick setae.

The genus appears to be an old and highly modified offshoot from a New World *Ptomaphagus* ancestor.

Genus *Adelopsis*

Adelopsis Portevin, 1907: 71. Type species *A. heterocera* Portevin. Jeannel, 1936: 59.

Diagnosis. The genus is very difficult to separate from *Ptomaphagus* by external characters. The species are generally smaller and broader than *Ptomaphagus.* The diagnostic feature lies in the short, thick, blunt aedeagus, often with complicated sculpture at the tip. Sexual dimorphism in the elytral apex is absent in the United States species.

Description. Length 1.7–3.5 mm. Form elongate oval, compact, convex. Color light to dark brown. Pubescent with numerous short recumbent golden hairs. Head finely punctured. Eyes normally large, to absent; in United States species eye width is 1/2 of width of head from antennal base to head margin across eye. Antenna short, compact, not reaching base of pronotum when laid back. Maxillary palp last article as long as preceding, conical, thinner. Pronotum wider than long, sides arcuate, striae distinct and coarse. Elytra gradually tapering to apex in both sexes in United States species; external apical angles rounded; sutural angles rounded; apex truncate; striae distinct, oblique. Wings present or absent, absent in all United States species. Mesosternal carina low, notch distinct. Legs short and compact, comb of spines limited to apex of tibiae, protibial apex oblique in males, rounded in females; tarsi swollen only in males on protarsi. Aedeagus short, stout, blunt, often with complex sculpturing at tip, orifice cutting to dorsal side through left side of aedeagus; internal sac with variable stylet, with short stylet in United States species. Parameres fused to aedeagus. Spiculum gastrale short, thick; less than 1/4 projecting beyond anterior end of genital plates. Spermatheca thin and curved in United States species, undescribed for other species.

Ecology. Members of the genus are either moist forest litter inhabitants or forest soil inhabitants. A few are known to inhabit caves, but do not show modifications for cave life. Those species with no wings and small or functionless eyes are probably scavengers in deeper litter, and in soil. They are rarely collected except by sifting litter. I have taken them in Central America and the United States by Berlese funnels and baited pitfall traps.

Distribution. Except for the species later discussed from Mt. Mitchell, North Carolina, all species previously described were from Mexico and South America. The following list gives recognized species, and locality or range. References are Jeannel (1936) and Szymczakowski (1961, 1963, 1968 and 1969b):

ascutellaris (Murray) 1856; Caracas, Venezuela
asper Jeannel 1936; Brazil (São Paulo; Alto da Serra. Santa Catharina; Blumenau). Paraguay
asperoides Szymczakowski 1963; Brazil (São Paulo)

bellator Szymczakowski 1968; Peru (Dep. Cuzco; Cajon, Bergland. Cosnipata-Ebene)
bernardi Portevin 1923; Brazil (Rio de Janeiro; Teresopolis. São Paulo; Alto da Serra)
bordoni Jeannel 1964; Venezuela (Merinda Prov., Capaya, Cueva Alfredo Jahn)
braziliensis Jeannel 1936; Brazil (Santa Catharina; Blumenau)
bruchi Pic 1926; Argentina (Buenos Aires)
brunneus Jeannel 1936; Colombia
darwini Jeannel 1936; Uruguay (Maldonado)
exiguus (Kirsch) 1870; Brazil. Columbia (near Bogota)
filicornis Jeannel 1936; Colombia
grouvellei Jeannel 1936; Brazil (Bahia, Rio de Janeiro, São Paulo)
heterocerus Portevin 1907; Bolivia (Cochabamba)
insolitus Szymczakowski 1961; Brazil (Santa Catharina; Nova Teutonia)
linaresi Szymczakowski 1969b; Venezuela (Cueva del Guacharo at Caripe)
luculentus Szymczakowski 1963; Brazil (São Paulo)
ovalis Jeannel 1936; Venezuela
ruficollis (Portevin) 1903; Bolivia (Cochabamba)
simoni (Portevin) 1903; Brazil (São Paulo; Alto da Serra). Mexico (Coatepec). Venezuela (Tovar and Rancho Grande)
triangulifer Szymczakowski 1961; Brazil (São Paulo. Santa Catharina; Nova Teutonia)

Though only one Mexican specimen and no Central American material is reported in the literature, the genus occurs in these areas. I have collected it in Mexico, Guatemala, Costa Rica, and Panama. I have also seen many *Adelopsis* taken by H. Dybas in Panama.

The genus has not previously been recognized from the United States. Besides the following species, here transferred to *Adelopsis,* I have seen material of at least six other species from Alabama, Georgia, Tennessee, North Carolina, West Virginia, and New Mexico.

Adelopsis mitchellensis (Hatch)
Figures 17, 18, 98, 139, 198

Adelops mitchellensis Hatch, 1933: 208. Holotype male and allotype female in AMNH, seen. Type locality: North Carolina, Black Mountains.
Ptomaphagus (*Adelops*) *mitchellensis,* Jeannel, 1936: 93; 1949: 99. New Combination.

Diagnosis. This is at present the only described *Adelopsis* in the United States. It is distinguishable from the undescribed species only by the characters of the aedeagus and spermatheca.

Description. Length 2.3–2.6 mm. Width 1.2–1.3 mm. Form oval. Color yellowish to dark reddish brown. Head sparsely punctured. Eyes reduced, pigmented, faceted; head width across eye from antennal base to margin 2.5 times eye width. Antennae (Fig. 98) short, compact; club darker, flattened, reaching middle of pronotum when laid back; segment III shorter than II; segments VI–X wider than long; VIII over twice as wide as long. Pronotum widest 1/3 before base; wider than elytra; 1.45 times as wide as long; hind angles acute; hind margin straight; striae composed of coarse punctures; pubescence moderate in length and amount. Elytra widest at base; 1.15 times as long as wide; external apical angles rounded; apex slightly oblique; striae oblique to suture; pubescentlike pronotum. Wings absent, elytra fused. Mesosternal carina low, notch present. Legs short; protibiae bowed-in; mesotibiae bowed-out; metatibiae straight. Aedeagus (Fig. 17) thick, tip pointed and thin; in dorsal view (Fig. 18) tip blunt; orifice on dorsal surface, right side of tip in dorsal view broad and dorsoventrally flattened, underlying left side. Spiculum gastrale short and thick, less than 1/4 projecting beyond anterior edge of genital plates (Fig. 198). Spermatheca (Fig. 139) simple curved tube, slightly swollen at anterior end, curved with thin crest at posterior end.

Variation. Differences appear in slide mounts of the aedeagus, usually a bending of the flattened plate of the right side of the aedeagus (arrow, Fig. 17) so that some of its dorsal face shows, giving an impression of a broader tip.

Field notes. The only habitat data is from a specimen I collected in a carrion-baited pitfall trap at 6400′ elev. in the balsam forest of the summit of Mt.

Mitchell. Another was taken at 4500′–6000′ elev. (INHS). Other specimens were probably taken by sifting litter and moss. Berlese funnel extraction of litter is probably the best method of recovering this species.

Seasonality. The only available information is that adults have been taken in April, and July through September. Larvae are unknown.

Distribution. Known only from the Black Mountains (and Mt. Mitchell) of Yancey County, North Carolina. I have seen 3 males and 6 females from this area (AMNH, FMNH, INHS, SBP, USNM).

Distributional comments. A second but undescribed species of *Adelopsis* occurs on Mt. Mitchell. This species, upon preliminary study, seems to have a much greater range, extending from Mt. Mitchell southwestward through the Smoky Mountains to northeastern Alabama. The species can be separated only by dissecting out the aedeagus and spermatheca.

Genus *Synaulus*

Synaulus Portevin, 1903: 157. Type species *S. agilis* (Lucas).

Characterization of genus. Length 2.0–2.5 mm. Shape very wide and convex. Color dark brown. Head retractable; eyes large. Antennae short, compact, club wide and flattened. Pubescence short, golden, recumbent. Prothorax and elytra covered with fine transverse striae. Winged. Legs very short, retractable under body, femora wide and flattened. Sexual dimorphism present in elytral apex and slightly in protarsi. Aedeagus like European *Ptomaphagus.*

Species. Two species are named and described, *agilis* (Lucas) 1849 and *pruinosus* (Reitter) 1881.

Ecology and distribution. The genus is known only from northern Algeria and Tunisia. Searching has not produced it in Morocco. It is a myrmecophile in nests of *Aphaenogaster testaceophilis* Lucas. Its role in the ant nest is not known, but the compact body suggests that the beetles have need of protection. They may simply be tolerated, feeding on nest debris.

The genus appears to have evolved from an ancestral European *Ptomaphagus.*

Genus *Ptomaphagus*

Ptomaphagus Illiger, 1798: 84. Type species *P. sericeus* Panzer.

Diagnosis. Aedeagus long and thin, orifice on dorsal surface, cutting left side of aedeagus. Elongate oval body with recumbent hairs, not broad and flattened with flattened legs and antennae and not living with ants.

Distribution. The genus occurs abundantly in the Nearctic and Palearctic regions, and infrequently in the Neotropical Region. One species is known at the edge of the Oriental Region.

Description. Few of the Old World species are available for study in this country. Information on them has been drawn from Jeannel (1936) and Szymczakowski (1964). Length 1.7–6.0 mm. Winged or wingless. Shape generally oblong, or elongate oval, rarely ovoid. Pronotum transversely striate, except in a few North American cave species in which the striae are reduced to random punctures on the disc. Elytra with striae oblique to the suture, except in *schwarzi* and some *nevadicus* in North America in which the striae are transverse to the suture. Pubescence golden, fine, recumbent. Head wide with an occipital carina. Epistome fused with front. Maxillary palps with last segment about as long as preceding. Eyes large, except in some North American species. Antennae with third segment always longer than wide.

Pronotum transverse, usually as wide as elytra, measuring widths at base or near base. Pronotal sides generally little rounded in hind half. Elytral sides narrowing posteriorly, slightly curved, their apical margin often truncate. In some North American species the elytral apex is

oblique and the female sutural angle is sharp. Sutural striae entire.

Mesosternum with flattened carina along midline, carina with free edge lightly to strongly rounded. Mesepisternum separated from mesepimeron by strong suture. Mesepimeron large, about as long as wide, its outer edge longer than the inner (Fig. 10). Metepisternum well developed, triangular or trapezoidal.

Anterior tibiae with comb of short equal spines occupying apical border, absent on external border (Fig. 14). Summit of meso- and metatibiae armed with two internal spurs and a comb of short equal spines replacing the outer spurs. Tarsi normal. Male with dilated protarsi (Fig. 14) and hind tibiae sometimes curved and thickened in distal portion. Female protarsi narrow (Fig. 13). First segment of mesotarsi narrow in both sexes.

Aedeagus form very regular, always long and thin, flattened dorsoventrally; apex with simple structure, triangular or ogival, sometimes with a small terminal button (bifid in *P. divaricatus* Jeannel); apical orifice on dorsal surface, cutting left edge; generally 7 setae on ventral surface of each side of tip. Parameres thin but always well developed, a little shorter than the aedeagus, with 3 setae on tips. Genital segment with triangular plates enclosing spiculum gastrale for part of its length.

Spermatheca with central shaft, slender posterior end often with knob, and curve at anterior end. (This has proved to be of great value in determining species in North America. It has been illustrated and described only for three European species by Kevan (1963). I have found Kevan to be correct in predicting that the spermatheca would prove to be of use throughout the tribe in distinguishing the females of species, which are difficult to identify by external characters alone.)

Distribution. The genus is widespread, containing many species that can be grouped into four subgenera. The subgenus *Ptomaphagus* is Palearctic, with its principal center of distribution in Europe. A few species are known to inhabit eastern Asia and Japan. One species occurs at the northern edge of the Oriental Region. A second large subgenus, *Adelops,* inhabits North and Central America. The remaining two subgenera contain two species each. They are *Merodiscus* of Yugoslavia and Rumania, and *Tupania* of Mexico and Brazil. The subgenera may be separated by the following key adapted from Szymczakowski (1961).

KEY TO SUBGENERA OF *PTOMAPHAGUS*

1a. Antennal club long, beginning with segment IV (Fig. 134) or at the summit of III ... 2
1b. Antennal club normal, beginning with segment VI or VII (Figs. 98–133) ... 3
2a. Segment II very short, much shorter than III. Pronotum as wide as elytra. Tarsi robust, first metatarsal segment 4–5 times as long as wide. Europe ... *Merodiscus*
2b. Segment II normal, slightly longer than III. Pronotum clearly narrower than elytra. Tarsi thin, first metatarsal segment 7 times as long as wide. Neotropical ... *Tupania*
3a. Legs rather robust, meso- and metatarsi thick, laterally flattened. Male anterior tibiae strongly dilated at summit, anterior tarsi wide. Palearctic ... *Ptomaphagus*
3b. Legs slender, meso- and metatarsi slender and not flattened. Male anterior tibiae long and not dilated, anterior tarsi longer. North and Central America ... *Adelops*

Comments on subgenera. Tupania and *Merodiscus* are well defined. This is not the case for *Adelops* and *Ptomaphagus* s. str. The differences between the two are seemingly mostly subjective impressions of Jeannel. From the material I have seen of European species, Jeannel's impressions seem to be at least mostly correct. Nevertheless, these two subgenera presently have good geographical utility. A critical evaluation of the validity of these two subgenera can be undertaken only with the later study of abundant Palearctic material. Szymczakowski (1961: 147) has noted that the North American species *brevior* and *consobrinus* show a transition from *Adelops* to *Ptomaphagus* s. str. This might be interpreted as a suggestion of the ancestral

stock and direction of migration from the Nearctic to the Palearctic Region.

Subgenus *Merodiscus*

Subgenus *Merodiscus* Jeannel, 1934: 162. Type species *Ptomaphagus validus* Kraatz.

Diagnosis. Easily distinguished by the small globose second antennal segment, and the much longer third segment.

Species and distribution. Two species are known. They are *validus* (Kraatz) 1852 from Rumania and Yugoslavia (seen in FMNH), and *biharicus* Jeannel 1924 from Rumania.

Ecology. Known only from under leaves and stones in forests.

Subgenus *Tupania*

Subgenus *Tupania* Szymczakowski, 1961: 146. Type species *Ptomaphagus forticornis* Matthews, 1888.

Diagnosis. Easily distinguished by the antennal club beginning with segment IV (Fig. 134).

Species and distribution. The subgenus contains only two named species, *forticornis* Matthews 1888 from Cordova, Mexico (type in BMNH, seen), and *flabellatus* Szymczakowski 1961 from Bocaina (near São Paulo) (allotype and 10 paratypes seen from PISZ), and Santa Catharina, Brazil. I have seen a broken female of a third species from Tucano, Amazonas State, Brazil, taken at 1500 m by J. & B. Bechyne, 28.iv.1964, in the Universidad Central de Venezuela, Facultad de Agronomia, Instituto de Zoologia Agricola collections at Maracay, Venezuela.

Supplementary descriptive notes on P. flabellatus. The metatibial spurs are proportionately longer than in *Adelops, flabellatus* having the longest spur 0.27 the length of the metatibia and 0.77 the length of the first metatarsomere (which is .44 × .08 mm). The metasternum is generally longer than in *Adelops,* in *flabellatus* its width (same reference axis as for entire beetle) being 1.4 times the length. The aedeagus (lateral view, Fig. 77) is basally bent, and the spermatheca (Fig. 140) is similar to those of the *cavernicola* group of *Adelops.* The male genital segment does not differ in a characteristic way from that generally found in *Adelops.*

Ecology. At least one of a series of 15 from São Paulo was taken under a cadaver (the kind of the cadaver is not mentioned). The Mexican species probably came from mesic forest litter in the region. I was unable to collect any in a week of field work near Cordova and Orizaba in July, 1969.

Subgenus *Ptomaphagus* sensu strictu

Diagnosis. Antennal club beginning with segment VII. Palearctic, with one Oriental species. Difficult to separate from the North American subgenus *Adelops,* except by the characters mentioned in the above key.

Species and distributions. Twenty-two species are recognized from Europe and Asia. The following is a checklist of these species and their general ranges. This list has been mostly compiled from Jeannel (1936) and all earlier references to descriptions can be found in that work. Sokolowski (1957) has been followed concerning synonymies of names used by Jeannel. I thank Dr. Waclaw Szymczakowski of Krakow, Poland, for his kind aid in providing corrections and additions to this list.

amamianus Nakane 1963; Japan
artizensis Jeannel 1934; Sardinia
caucasicus Jeannel 1934; western Caucasus
chendai J. Müller 1921; Italy, Albania, Yugoslavia
circassicus Reitter 1888; western Caucasus, Crimea
clavilis Reitter 1884; Sardinia, Sicily, Majorca
dacicus Jeannel 1934; Rumania
divaricatus Jeannel 1934; Yugoslavia, Albania
kuntzeni Sokolowski 1957; Japan, NE Burma
medius Rey 1889; western, central, and northern Europe
pius Seidlitz 1887; Italy
pyrenaeus Jeannel 1934; France
rhagianicus Sbordoni 1967; Iran

sardus Seidlitz 1887; Sardinia
sericatus Chaudoir 1845; central and southeastern Europe
sibiricus Jeannel 1934; Vladivostock, Japan
subtruncatus Mäklin 1881; Siberia
subvillosus Goez 1777; western and central Europe
tauricus Jeannel 1934; Turkey, Syria
tenuicornis Rosenhauer 1856; Spain, N. Africa
vallombrosae Seidlitz 1887; Italy
variicornis Rosenhauer 1847; Europe

Ecology. Little information is available on the habits and habitats of Palearctic *Ptomaphagus.* Jeannel (1936) provides as much information as can be generally found. The species are usually associated with forested areas. Mountain habitats are indicated for *subvillosus,* and for *kuntzeni* (taken in flight at 2000 m in Burma). Several species have been taken in caves or cave entrances (*chendai, pyrenaeus,* and *sericatus*), though none of these species exhibits cave adaptations. Moss and rotting leaves are indicated for *pius, sericatus, subvillosus, valombrosae,* and *variicornis,* and flood debris has given *tenuicornis.* Small invertebrate bodies (snails, hemipterans, scorpions) have yielded *sericatus* and small mammal cadavers *subvillosus.* Nests of moles, shrews, and hamsters have yielded *sericatus* and *variicornis,* and rabbit nests *subvillosus* and *variicornis.* An anthill yielded the single specimen of *subtruncatus* and *Lasius* anthills have yielded *sericatus* and *tenuicornis.* Malaise traps have taken *kuntzeni* in flight in Burma. In all of the above cases, the beetles show themselves to be lovers of dark moist places, where they are probably feeding as scavengers on decaying plant and animal matter.

Subgenus *Adelops*

Adelops Tellkampf, 1844: 318. Type species *Adelops hirtus* Tellkampf.

Diagnosis. Antennal club beginning with segment VII. North and Central American species. Difficult to separate from the Palearctic subgenus *Ptomaphagus;* see comments above.

Species. A total of 36 species from North and Central America are here recognized and named. Of these species, 44.5 percent are troglobites. Twelve troglobitic species are in the southeastern United States, one in the southwestern United States, two occur in Mexico, and one in Guatemala. An additional 30.5 percent are less specialized hypogean species living in underground environments such as caves, deep humus, and animal burrows from southern Canada to Panama. The remaining 25 percent are epigean in forest litter from southern Canada to Guatemala. An estimated seven species are additionally recognized but are too poorly known to merit description.

Species groups. Jeannel (1949) proposed a system of six species groups for *Adelops.* This was partly followed by Barr (1963). I do not think that Jeannel's groups are sound. Several of the external characters used by him have arisen more than once, and others are convergent adaptations to similar habitats. I prefer a system using internal genital structures, which I believe to be a more sound approach in *Adelops.* I have used as a group name that of the oldest species in the group. The groups are (1) the *hirtus* group, with a reversed "J"-shaped spermatheca, containing the 12 cave-specialized species of the eastern United States, and one edaphophile species from the Ozark region; (2) the *consobrinus* group, with a reversed "S"-shaped spermatheca, with 10 species in the United States, southern Canada, and western Mexico, and one in Guatemala; and (3) the *cavernicola* group, with a reversed "S"-shaped spermatheca with a coil at the posterior end, with 10 Mexican species, and one ranging from northeastern Mexico through much of the eastern and southern United States. Three species, known only from males, are not assigned to a group.

The species groups are not included in the following species key. The groups are characterized above, based on female spermathecae. These groups can be criti-

cized because of seemingly undue emphasis placed on just this one character. However, in justification, I think the chances for convergence through selection to similar forms in the spermathecae of distantly related species are less than for convergences in external structures of an obviously adaptive significance. The spermathecae are less directly affected by selection than other structures. They are useful because they are both conservative enough in overall shape to indicate major groups, and complex enough to indicate specific differences. As a second defense for the groups, I suggest that their included species share broadly common characteristics of distribution and ecology. In this way they are later very useful in discussions of phylogeny, zoogeography, and evolution. Lastly, I could find no other character or even group of characters that I thought had as comparable and potentially reliable an information content.

Species key. The following key will serve to separate the species. The key is an aid to identification, and does not indicate relationship. The species groups are not used here because this would require a dissection of the specimen before the first couplet could be approached. The species are discussed later in the text under the group in which I have placed them. The key does not include *championi* from Guatemala. The key is not easy to work, because there are few distinct, unequivocal external characters in *Adelops*. Quite often the best character is the species distribution, and this has been used in the key. Until a worker gains familiarity with the subgenus, or has a comparative or synoptic collection to work with, positive determinations of the populations sampled by a collector will usually require dissections, preferably of both males and females.

A Key to the North American Species of *Ptomaphagus* (*Adelops*)

1a. Eyes unpigmented, greatly reduced; troglobites 2
1b. Eyes pigmented, not reduced or only partly so, may or may not be cavernicoles 19
2a. Troglobites in caves in Mexico 3
2b. Troglobites in caves in the eastern United States 4
3a. In caves in central Nuevo León .... *gypsum*
3b. In caves in Sierra de Guatemala, Tamaulipas .... *troglomexicanus*
4a. Aedeagus long, thin, straight (Figs. 35, 37, 38) 5
4b. Aedeagus thicker, curved (Figs. 21–26) 7
5a. In caves in west-central Kentucky .... *hirtus*
5b. In caves in Illinois or Tennessee 6
6a. In caves in Monroe County, Illinois .... *nicholasi*
6b. In caves in central Tennessee, on southeastern edge of Nashville Basin .... *hubrichti*
7a. Aedeagus upturned at tip (Fig. 26) .... *hazelae*
7b. Aedeagus straight or downturned at tip 8
8a. Mesosternal carina high (Figs. 83–86) 9
8b. Mesosternal carina low (Figs. 79–82, 87–90) 12
9a. Ventral margin of carina sinuous (Fig. 84) .... *fiskei*
9b. Ventral margin of carina straight 10
10a. Antennal segments II and III subequal (Fig. 108); caves of DeKalb County, Alabama, and Dade County, Georgia .... *whiteselli*
10b. Antennal segment III clearly longer than II 11
11a. Pronotum widest at base; central Tennessee .... *barri*
11b. Pronotum widest 1/3 before base; Blount County, Alabama .... *walteri*
12a. Pronotal sides parallel behind 13
12b. Pronotal sides not parallel behind 17
13a. Spermatheca with thin curved central shaft (Fig. 152) .... *valentinei*
13b. Spermatheca with stout central shaft (Figs. 142–146) .... *loedingi*, 14
14a. In caves west of the Flint River, Madison County, Alabama .... *loedingi loedingi*
14b. In caves east of Flint River 15
15a. In caves in Keel Mountain (in Madison and Jackson counties) between Flint and Paint Rock rivers .... *loedingi longicornis*
15b. In caves in Jackson County east of Paint Rock River 16
16a. In cave(s) in Tater Knob, immediately N & NW of Scottsboro .... *loedingi solanum*
16b. In cave(s) in July Mountain, 2–5 miles SW of Scottsboro .... *loedingi julius*
17a. Spermatheca shaft undulating, without

knob on posterior end (Fig. 157); caves in Bishop Mountain, Marshall County, Alabama .... *episcopus*
17b. Spermatheca shaft straight, or without knob on posterior end (Figs. 153–156) .... *hatchi*, 18
18a. In Caney Hollow Cave at edge of Nashville Basin, in western Franklin County, Tennessee .... *hatchi fecundus*
18b. In caves of escarpment of Cumberland Plateau, in Grundy and eastern Franklin counties, Tennessee, and Jackson and Madison counties, Alabama .... *hatchi hatchi*
19a. Eyes distinctly reduced, their horizontal diameter equal to the space between their anterior margin and the antennal socket 20
19b. Eyes normal or slightly reduced, with diameter greater than width of eye-antennal socket space 23
20a. Antennae short, not extending far into elytra when laid back 22
20b. Antennae long, extending into first 1/4 of elytra when laid back 21
21a. Mesosternal carina very high (Fig. 93); Guatemala; troglobite .... *giaquintoi*
21b. Mesosternal carina low; Panama; high montane forests .... *talamanca*
22a. Ozark region of United States .... *shapardi*
22b. In high montane forests of Querétaro, Mexico .... *meximontanus*
23a. Male metafemur with tooth on hind margin (Figs. 15, 16) 24
23b. Male metafemur smooth on hind margin 25
24a. Fully winged; female elytral apex not drawn out; widespread in western United States .... *fisus*
24b. Wings reduced to 3/4 elytral length; female elytral apex drawn out; cavernicole in Grand Canyon, Arizona .... *cocytus*
25a. Spermatheca simple reversed "S" shape; mostly species inhabiting United States 26
25b. Spermatheca a more complex reversed "S" shape with additional coil at posterior end (Figs. 187–197); species mostly Mexican 32
26a. Mesosternal notch deep, rounded (Figs. 95, 96) 27
26b. Mesosternal notch shallow, right-angled 28
27a. Spermatheca broadly flattened in anterior end (Figs. 180–183) .... *brevior*
27b. Spermatheca narrow in anterior end (Fig. 185) .... *ulkei*
28a. Edge of genital plates bordering genital orifice with concavity (Figs. 203, 206) 29
28b. Edge of genital plates bordering genital orifice straight or convex 30
29a. Spermatheca very broadly flattened at both ends (Figs. 173–174); California .... *californicus*
29b. Spermatheca very thin, not flattened (Figs. 178, 179); southeastern United States .... *consobrinus*
30a. Female elytral apex sinuous; western and Gulf states 31
30b. Female elytral apex obliquely truncate, not sinuous; Gulf Coastal states .... *texanus*
31a. Eyes reduced, 1.15 times width of eye-antennal socket space; spiculum gastrale short (Fig. 201); Florida .... *schwarzi*
31b. Eyes normal to slightly reduced, 1.3–1.9 times as wide as eye-antennal socket space; spiculum gastrale long and thin (Fig. 205); North America west of the Mississippi River .... *nevadicus*
32a. Female elytral tips drawn out, sutural angle sharp (Fig. 135) 33
32b. Female elytral tips not drawn out, sutural angle rounded (Figs. 136–138) 35
33a. Eyes very large, antennal segment II distinctly shorter than III; in forests of Sierra Madre de Oaxaca, Mexico .... *oaxaca*
33b. Eyes somewhat reduced, antennal segments II and III subequal; cavernicole; northeastern Mexico and southern and eastern United States .... *cavernicola*, 34
34a. Eye width 2.0–2.9 times width of eye-antennal socket space; widely distributed .... *cavernicola cavernicola*
34b. Eye width 1.5–1.75 times the width of the eye-antennal socket space; Nuevo León, Mexico .... *cavernicola aditus*
35a. Eyes more coarsely faceted and somewhat reduced, their horizontal diameter 1.9–2.0 times the width of eye-antennal socket space; high forests of Chiapas, Mexico .... *altus*
35b. Not above combination 36
36a. Aedeagus tip blunt in dorsal view (Figs. 63, 71) 37
36b. Aedeagus tip pointed in dorsal view (Fig. 67); forests of Sierra Madre de Oaxaca .... *newtoni*
37a. Aedeagus shorter and thicker (Fig. 62); cavernicole in Sierra de El Abra, Tamaulipas and Nuevo León, Mexico .... *elabra*
37b. Not above combination 38
38a. Aedeagus in lateral view with ventral button at tip (Fig. 72); cavernicole; Guerrero, Mexico .... *spelaeus*
38b. Not above combination 39
39a. Spermatheca longer and thinner at anterior end (Fig. 197); montane forests of Chiapas, Mexico .... *jamesi*

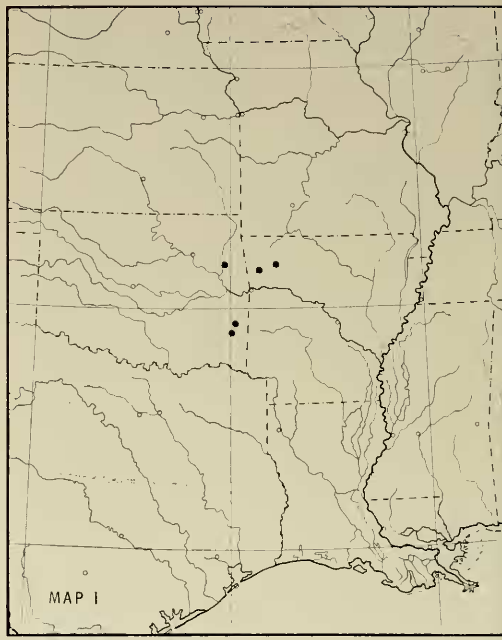
39b. Spermatheca shorter and thicker at anterior end (Fig. 193); middle and low elevation forests of Nuevo León, Mexico .... *leo*

The *Hirtus* Group

Diagnosis. Spermatheca shaped like a reversed "J," often with the posterior end bent to the left, and the anterior end neither swollen nor broadly flattened (Figs. 141–163).

Description. Shape elongate oval. Color medium brown to light brown or reddish brown. Eyes reduced in all species to small unpigmented areolae with a few facet remnants present (Fig. 6) except in *shapardi* (Fig. 5). Antennae medium or long. Pronotum with hind angles acute. Elytra with external apical angles rounded, apex truncate in females and rounded in males. Wings reduced to tiny elongate scales. Mesosternal carina medium or high. Aedeagus straight and thin, to slightly curved.

The group contains one edaphophilic species from the Ozark region of the central United States, and twelve troglobitic species (two of which are divided into six subspecies) from the southeastern United States. Reproductive seasonality in the troglobites probably does not exist in individuals living away from the fluctuating environment of cave entrances (winter lowering of temperature and humidity).



Map 1. Distribution of *Ptomaphagus* (*Adelops*) *shapardi*, a wingless, small-eyed, soil and cave inhabitant of western Arkansas and eastern Oklahoma.

Ptomaphagus shapardi Sanderson
Figures 5, 19, 20, 78, 99, 141; Map 1

Ptomaphagus (*Adelops*) *shapardi* Sanderson, 1939b: 121. Holotype male and allotype female in INHS, seen. Type locality: Oklahoma, Cherokee County, Dresser Cave (5 mi. N Ft. Gibson). Jeannel, 1949: 101. Barr, 1963: 53.

Diagnostic combination. This is the only *Ptomaphagus* known from the southwestern Ozark region having eyes reduced to one-half the width of the head from the antennal base to the margin across the eye.

Description. Length 2.4–2.8 mm. Width 1.2–1.4 mm. Color yellowish brown to dark brown. Head finely punctured; eyes reduced, faceted, pigmented (Fig. 5); width of head from antennal base to margin across eyes twice width of eye on same line; ridge present from antennal base to top of eye. Antennae (Fig. 99) medium length, reaching base of pronotum when laid back, club beginning with segment VII; segment I longest; segments II and III subequal; IV, V and VI progressively shorter, wider; VII longer than wide; VIII transverse; IX quadrate; X broader than long; XI longer than broad. Pronotum at base 1.5 times as wide as long; widest 1/3 before base; hind margin straight; striae on disc composed of coarse setigerous punctures. Elytra elongate, sides parallel in anterior half, narrowing in posterior half; as wide as pronotal base; 1.5 times as long as wide. Mesosternal carina (Fig. 78) low, notch right-angled. Aedeagus (Fig. 19) in lateral view slightly curved, gradually narrowing to slender tip; tip in dorsal

view (Fig. 20) with broad point. Spermatheca (Fig. 141) with curved shaft, posterior knob bent to left, opening to right, anterior hook small, no crest.

Variation. None noted.

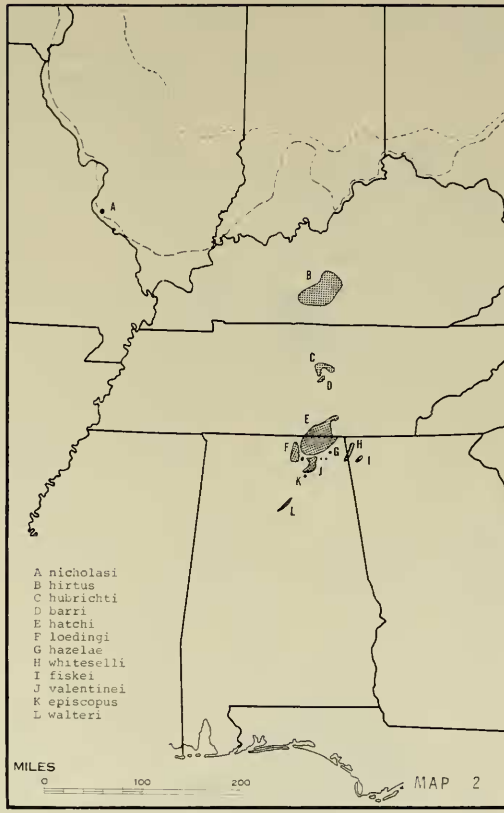
Collecting notes. The type series of 26 specimens came from gravelly debris, in total darkness, about 50 feet from the cave entrance (Sanderson, 1939b). One came to a bait trap in an Arkansas cave, and one to a carrion trap at a pile of rocks in an Oklahoma forest. Berlese collecting has taken them in litter in Oklahoma, and three times in deep litter in Devils Den State Park, Arkansas.

Seasonality. Adults have been taken in January, June, July, and December. Tenerals are known from January and June collections. Larvae are unknown. Reproduction probably can occur throughout the year in protected environments such as caves and deep litter pockets.

Distribution. The species is known from the southwestern Ozark region of Oklahoma and Arkansas, and the Ouachita Mountains of Oklahoma (Map 1). Additional collecting in litter in spring and early summer will undoubtedly widen the range. I have seen 31 specimens from the following five localities: ARKANSAS. *Washington County:* Devils Den State Park, Winslow, 6 (SBP, INHS); Finchers Cave, 10 mi. SE Fayetteville, 1 (INHS). OKLAHOMA. *Cherokee County:* Dresser Cave, 5 mi. N Ft. Gibson, 19 (INHS, MCZ, TCB). *Leflore County:* Cedar Lake Camp, 10 mi. SSW Heavener, 1 (SBP); Winding Stair Mt., 1600′, 12 mi. SSW Heavener, 4 (SBP).

Distributional comments. The Arkansas River is a major potential dispersal barrier crossing the range of this flightless species.

The flightless condition, small eyes, and collecting localities suggest that the species is an inhabitant of forest soil and deep litter. Forests providing such habitats do not extend farther west than the species' western range limits in Oklahoma. Most of Arkansas and Missouri are suitably



Map 2. Distribution of the troglobitic (blind, cave-adapted) *Ptomaphagus* (*Adelops*) in the United States. These species are concentrated in northeastern Alabama and adjoining parts of Georgia and Tennessee. The long-dashed line represents the maximum extent of glaciation of the Illinoian ice sheet. The short-dashed line represents the maximum extent of the Wisconsin ice sheet.

forested, however. The species may occur in such a larger range, but this is unknown because little or no deep litter and soil collecting has been done in the Ozarks.

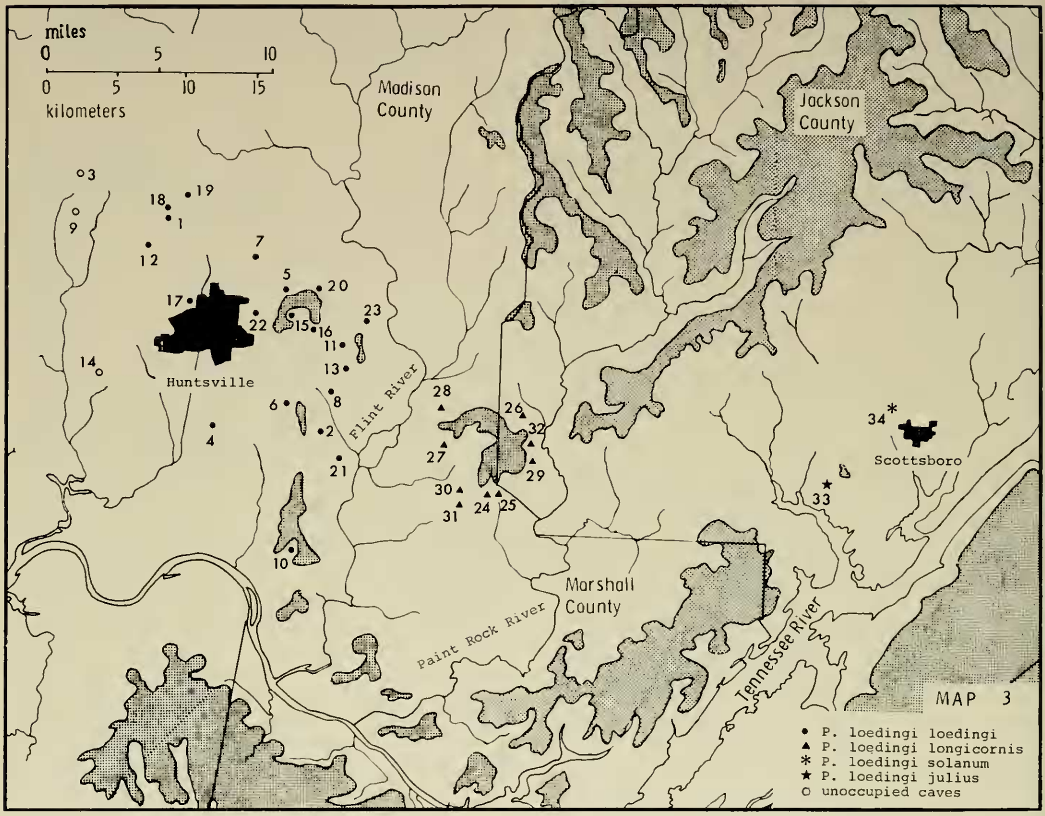
Ptomaphagus loedingi loedingi Hatch
Figures 21, 79, 100, 142, 143; Map 3

Adelops lödingi Hatch, 1933: 209. Holotype male and allotype female in USNM (no. 43763), seen. Type locality: Alabama, Madison County, Shelta Cave.

Ptomaphagus (*Adelops*) *lödingi*, Jeannel, 1936: 93; 1949: 104.

Ptomaphagus (*Adelops*) *loedingi*, Barr, 1963: 57.

Ptomaphagus (*Adelops*) *valentinei jonesi* Jeannel,



Map 3. Distribution of *Ptomaphagus* (*Adelops*) *loedingi*, a troglobitic species of northeastern Alabama. Stippling represents the Pottsville sandstone remnants of the Cumberland Plateau. Caves do not exist under this caprock. Consequently, the plateau remnants, as well as the large rivers and streams, represent barriers to subterranean terrestrial dispersal. Geology from Malmberg and Sanford (1963) and Adams et al. (1926). The localities are as follows: 1 Barclay Cave, 2 Buford Cave, 3 Burwell Cave, 4 Byrd Spring Cave, 5 Cold Spring Cave, 6 Canoe Cave, 7 Cave Spring Cave, 8 Drake Cave, 9 Ellis Cave, 10 Green Grotto, 11 Jett Cave, 12 Kelly Natural Well, 13 Lott Cave and Pitt Sinkhole Cave, 14 Matthews Cave, 15 Natural Well, 16 Sadler Spring Cave, 17 Shelta Cave, 18 Sinks Cave, 19 Spook Cave, 20 The Sinks, 21 Taploe Cave, 22 Toll Gate Natural Well, 23 Twin Caves, 24 Bee Sinkhole Cave and Moon Sinkhole Cave, 25 Butler Sinkhole and Chittimwood Cave, 26 Crossing Cave, 27 Goat Cave, 28 Grayson Spring Cave, 29 Greising Cave, 30 Hering Cave, 31 Labyrinth Cave, 32 Paint Rock Cave.

1949: 103. NEW SYNONYMY. Type in MNHN, Paris, not seen. Type locality: Alabama, Madison County, Pitts Sinkhole Cave.

Ptomaphagus (*Adelops*) *henroti ellipticus* Jeannel, 1949: 102. NEW SYNONYMY. Type male in MNHN, Paris, seen. Type locality: Alabama, Madison County, Shelta Cave. Barr, 1963: 56.

Diagnosis. Ptomaphagus loedingi is a polytypic species, containing four geographically disjunct subspecies, in caves in Madison and Jackson counties, Alabama. The species is characterized by an elongate and thin aedeagus; elongate antennae with segment III clearly longer than II; a low mesosternal carina; and a spermatheca with a curved shaft and a knob at the posterior end.

The nominate subspecies occurs only in caves west of the Flint River in Madison County. It is distinguished from the other subspecies by its spermatheca with a small posterior knob, and trace of a crest on the anterior end.

Description. Length 2.7–3.6 mm. Width 1.2–1.4 mm. Head finely, sparsely punctured. Width of head across eye from antennal base to margin 4 times width of eye. Antennae (Fig. 100) thin and long, reaching into first third of elytra when laid back; segment III longer than II, subequal to I; II subequal to IV; IV, V and VI progressively shorter and wider; VII elongate, conical; VII twice as wide as long; VIII wider than long; X and XI longer than wide. Pronotum at base 1.5 times as wide as long, widest at base, or slightly before; posterior margin parallel or only slightly arcing to hind angles; hind angles slightly acute; hind margin slightly sinuous; striae present but faint. Elytra slightly more narrow than pronotum; at base 1.5 times as long as wide. Mesosternal carina (Fig. 79) medium, notch absent or faint. Aedeagus (Fig. 21) gently arcing and narrow, narrowing gradually to tip. Spermatheca (Figs. 142, 143) with short stout shaft, posterior end slightly swollen into knob, opening to right, or ventral of right; anterior end with small hook, low crest.

Variation. The most conspicuous variation is in the posterior knob and direction of opening of the spermatheca. The proportion of length to thickness of the shaft also varies slightly between populations. These differences are seen in the spermatheca illustrations (Figs. 142–143). Gradation exists from one into the other shape in a clinal fashion.

Distortion that might be interpreted as variation is noticed frequently in this subspecies in permanent slide mounts of the aedeagus. The aedeagal tip appears broad, when twisted down by the cover glass.

The type male of *henroti ellipticus* Jeannel is a small individual of *P. loedingi loedingi,* if there is no doubt that it was collected in Shelta Cave. Its pronotal and elytral lengths and widths and their ratios (PW 1.02 mm at base; PL 0.73 mm; EL 1.43 mm; EW at base 1.05 mm; and EW at widest 1.07 mm) do not separate it from *loedingi.* The key character that Jeannel used to separate *henroti* and *loedingi* was the relative lengths of the third and second antennal segments. In the key of Jeannel (1949) I run the type male to *P. loedingi.*

Field notes. Baiting and trapping has gathered huge numbers of the beetles in a few caves. Walter Jones took 723 in traps in Natural Well in 1937. In an ecology study in 1965 in Barclay Cave I took 534 adults and 357 larvae. Baiting in Cold Spring Cave from 21 August to 14 September in 1968 yielded 1,673 adults, most of which were released. The beetles were originally taken on bat guano in Shelta Cave (Hatch, 1933: 209), but I have never found them on bat guano in any cave.

Seasonality. Laboratory cultures show these beetles to have no reproductive seasonality when maintained under constant cavelike conditions. Adults have been taken in every month except March and April. Larvae have been found throughout the summer. In 1965 larvae were most abundant in Barclay Cave in late August, suggesting a large hatch of eggs laid by a large number of adults two weeks earlier.

Distribution. The subspecies is known only from caves in Madison County, west of the Flint River (Map 3). I have seen 1,915 preserved adults from the following twenty-one localities: ALABAMA. *Madison County:* Barclay Cave, 588 (SBP, TCB, UANH); Buford Cave, 11 (UANH); Byrd Spring Cave, 57 (SBP); Cold Spring Cave, 31 (SBP, UANH); Canoe Cave, 2 (SBP); Cave Spring Cave (No. 60, Chapman Mt.), 37 (SBP, UANH); Drake Cave, 18 (UANH); Green Grotto, 2 (SBP); Jett Cave, 1 (UANH); Kelly Natural Well, 31 (UANH); Lott Cave, 22 (UANH); Natural Well, 725 (UANH); Pitt Sinkhole Cave, 93 (UANH); Sadler Spring Cave, 4 (UANH); Shelta Cave, 162 (CAS, TCB, UANH, USNM); Sinks (Simmons) Cave, 3 (TCB); Spook Cave, 6 (UANH); The Sinks, 91 (SBP UANH); Taploe Cave,

(UANH); Toll Gate Natural Well, 11 (UANH); Twin Caves, 21 (TCB, UANH).

Distributional comments. The range of the subspecies exists in limestones with no known extrinsic barriers to dispersal and gene flow. The range is roughly in a 17-mile long north-south line, west of the Flint River, from Spook Cave in the north to Green Grotto in the south (Map 3). The Flint River separates this series of populations from those of *P. loedingi longicornis* living in caves in Keel Mountain. The populations of *loedingi julius* and *loedingi solanum* lie even further to the east, beyond the Paint Rock River. These last two subspecies are also separated by intervening populations of *P. valentinei* and *P. hatchi.* I later suggest that the wide distribution of the species was gained by overland dispersal during Wisconsin time, and the subspeciation has occurred since then.

The northwestern limit of the range of *loedingi loedingi* must lie between Drake Mountain and Burwell Mountain where baiting has not taken specimens in Ellis Cave, and Burwell Cave. The western limits of the range do not reach Matthews Cave, as shown by baiting. To the south, the range is limited by the Tennessee River.

Ptomaphagus loedingi longicornis Jeannel
Figures 22, 80, 101, 144; Map 3

Ptomaphagus (Adelops) valentinei longicornis Jeannel, 1949: 103. New Combination. Holotype male in MNHN, Paris, not seen. Type locality: Alabama, Madison County, Cave Spring Cave (Hering Cave). Barr, 1963: 56.

Diagnosis. Known only from caves in Keel Mountain, an isolated remnant of the Cumberland Plateau, in Madison and Jackson counties, Alabama. The subspecies is clearly defined from other subspecies of *loedingi* only by the shape of the spermatheca, and by the extreme elongation of the third antennal segment as compared with the second.

Description. Like *loedingi loedingi* with the following exceptions: antennae (Fig. 101) with segment III markedly longer than II, II shorter than IV; VII to X more elongate; VIII longer than broad. Mesosternal keel low (Fig. 80). Aedeagus (Fig. 22) slender. Spermatheca (Fig. 144) with knob on posterior end, opening to right on dorsal surface; anterior end with small crest.

Variation. No variation has been noted within the subspecies.

Field notes. I have taken numerous specimens by baiting in Paint Rock Cave and Hering (Cave Spring) Cave, and by trapping in Crossing Cave.

Seasonality. Year-round reproduction is found in laboratory cultures of the beetles, and it undoubtedly occurs also in cave populations. Adults have been collected in February, March, July, August, and September, but this reflects only the activity of collectors, not the beetles. Tenerals were not present in the August 1968 collection of 188 adults. Larvae have been taken in caves only in July, August, and September.

Distribution. Known only from Keel Mountain, an isolated remnant of the Cumberland Plateau, in Madison and Jackson counties, Alabama. The mountain is bounded on the west by the Flint River, on the east by the Paint Rock River, and on the north and south by lowlands containing tributaries to both the Paint Rock and Flint rivers. I have seen 367 preserved specimens from the following 12 localities (Map 3): ALABAMA. *Jackson County:* Crossing (Stewart) Cave, 326 (SBP, TCB); Greising Cave, 2 (SBP); Paint Rock Cave, 12 (SBP). *Madison County:* Bee Sinkhole Cave, 4 (UANH); Butler Sinkhole, 6 (UANH); Chittimwood Cave, 2 (UANH); Goat Cave, 6 (UANH); Grayson Spring Cave, 2 (UANH); Hering (Cave Spring) Cave, 3 (UANH); Labyrinth Cave, 2 (UANH); Moon Sinkhole Cave, 2 (UANH).

Distributional comments. The subspecies is separated from *loedingi loedingi* to the west by the Flint River. To the north, east, and south *P. episcopus, valentinei,*

and *hatchi* occupy caves on the east side of the Paint Rock River. To the southwest, baiting in Morring Spring Cave and Clarks Bluff Cave have not taken *Ptomaphagus* in the isolated group of contiguous Meeks, Lemley, Mayo, and McKinney mountains.

Ptomaphagus loedingi julius new subspecies
Figures 23, 81, 102, 145; Map 3

Holotype male and allotype female in MCZ (no. 31902). Type locality: Alabama, Jackson County, House of Happiness Cave (4 mi. SW Scottsboro). Type data: 14.ix.1968, S. Peck. Paratypes: 83 with same data.

Diagnosis. Known only from House of Happiness Cave, in July Mountain. The subspecies is characterized the same as *loedingi loedingi,* but separated from it by the shape of the spermatheca.

Description. Similar in all respects to *loedingi loedingi* with the following exceptions: antenna (Fig. 102) with segments VI, VII, and VIII proportionately longer. Mesosternal carina (Fig. 81) more pronounced, but low, slight notch present. Aedeagus (Fig. 23) less curved. Spermatheca (Fig. 145) with swollen posterior end, no crest on anterior end.

Variation. None noted within the subspecies.

Etymology. Latin, *julius,* July, a noun in apposition, referring to July Mountain to which the subspecies is probably isolated.

Field notes. Six were found on *Neotoma* rat dung. A series of 85 was taken by baiting in the room about 30 meters from the cave entrance.

Seasonality. Seasonality is known only from two collections, made in August 1968. Five teneral adults were taken in the series of 85. Larvae are not known.

Distribution. The subspecies is known only from House of Happiness Cave, in July Mountain, Jackson County, Alabama (Map 3). I have seen 91 specimens.

Distributional comments. July Mountain is a remnant of the Cumberland Plateau. It is bordered on the southwest by the Tennessee River, on the northeast by Roseberry Creek and Roseberry Bottoms, and on the south and southwest by Sauta Creek. The possibility exists for dispersal in limestones to the northwest along Cotton Mountain and for contact with *P. hatchi* in the Plateau escarpment northwest of Larkinsville. This possibility can only be tested by baiting in the few caves known northwest of Larkinsville. No caves are known in Cotton or July mountains except House of Happiness Cave.

This population is 13 miles due east of the nearest population of *P. loedingi longicornis* in Keel Mountain. The intervening distance is occupied by both *P. valentinei* and *P. hatchi.* The distance to the northeast to Sheldons Cave, inhabited by *P. loedingi solanum,* is only 4.5 air miles. However, dispersal between these caves through limestone would involve a distance of at least 14 miles, around the head of Boxes Cove. Only one other population is known along this route, and it is of *P. hatchi,* in Indian Rocks Cave, in the head of Boxes Cove.

Ptomaphagus loedingi solanum new species
Figures 24, 82, 103, 146; Map 3

Holotype male and allotype female in MCZ (no. 31903). Type locality: Alabama, Jackson County, Sheldons Cave. Holotype data: 6.viii.1967, S. Peck, A. Fiske leg. Allotype data; 12.vii.67, S. Peck, A. Fiske leg. Paratypes: 16 from above locality; 4–8.iv.67, S. Peck, 2; 8.iv.67, S. Peck, 6; 6.viii.67, S. Peck, A. Fiske, 3; 14.ix.68, S. Peck, 1; 27.i.67, S. Peck, 1; 12.vii.67, S. Peck, A. Fiske, 3.

Diagnosis. The subspecies is known only from Sheldons Cave, 1 mile northwest of Scottsboro. It is characterized the same as *loedingi loedingi,* but separated from it by the shape of the spermatheca.

Description. Similar in all respects to *loedingi loedingi* with the following exceptions: Head. Eye remnant smallest of troglobitic *Ptomaphagus,* width of head

from antennal base to margin across eye 6–8 times width of eye. Antennae (Fig. 103) more elongate; segments VII, IX, and X proportionately more slender; VIII longer than wide in side view only. Pronotum widest 1/3 before base. Mesosternal carina (Fig. 82) higher, notch faint. Aedeagus (Fig. 24) wider through middle. Spermatheca (Fig. 146) with fairly straight central shaft; posterior end bent to left into offset knob, opening to right; anterior end with no crest.

Variation. None has been noted in this subspecies.

Etymology. Latin, *solanum*, potato, a noun in apposition referring to Tater Knob, in which the subspecies lives.

Field notes. Taken by baiting along the stream, and on the flow-stone in the first 20 meters of the cave.

Seasonality. Adults have been collected in January, April, July, August, and September. Tenerals are not known, and only one larva has been collected.

Distribution. Known only from the type locality (Map 3), a cave in Gasper Limestone, in Tater Knob one mile northwest of Scottsboro. I have seen 18 specimens from the type locality collected by myself in six visits to the cave in 1967 and 1968.

Distributional comments. Tater Knob is connected by limestones to the Cumberland Plateau escarpment near Skyline with no obvious barriers to subterranean dispersal. In a straight line distance, eight miles of limestone lie between Sheldons Cave, and the *P. hatchi* population in Indian Rocks Cave. Roseberry Bottoms and Roseberry Creek to the southwest of Sheldons Cave separate it from July Mountain and House of Happiness Cave, inhabited by *P. loedingi julius*.

Ptomaphagus barri new species
Figures 25, 83, 104, 147; Map 4

Holotype male and allotype female, in MCZ (no. 31887). Type locality: Tennessee, Cannon County, Henpeck Mill Cave, 22.viii.1967, S. Peck and A. Fiske. Paratypes: 55 with same data.

Diagnosis. Ptomaphagus barri is one of two blind *Ptomaphagus* living in caves in central Tennessee. It may be told from the other (*hubrichti*) by the second antennal segment being clearly shorter than the third, and the emargination in the basal third of the pronotum. Neither are found in *hubrichti.*

Description. Length 2.8–3.2 mm. Width 1.3–1.5 mm. Head smooth; width of head from antennal base to margin across eye 4.7 times width of eye. Antennae (Fig. 104) elongate, reaching into first third of elytra when laid back; segments I and III subequal, longer than II; VIII conical, longer than wide; IX and X 3/4 as wide as long. Pronotum at base 1.5 times as wide as long, widest at base, emarginate in basal third when viewed from above; hind margin sinuate; striae pronounced on disc. Elytra at base wider than pronotal base, widest 1/3 from base; 1.6 times as long as wide at base. Mesosternal carina (Fig. 83) strong, notch absent. Aedeagus (Fig. 25) slightly curved, widest at middle, slender at tip. Spermatheca (Fig. 147) with long slender central shaft, small knob on posterior end, irregular slender hook on anterior end with distinct crest.

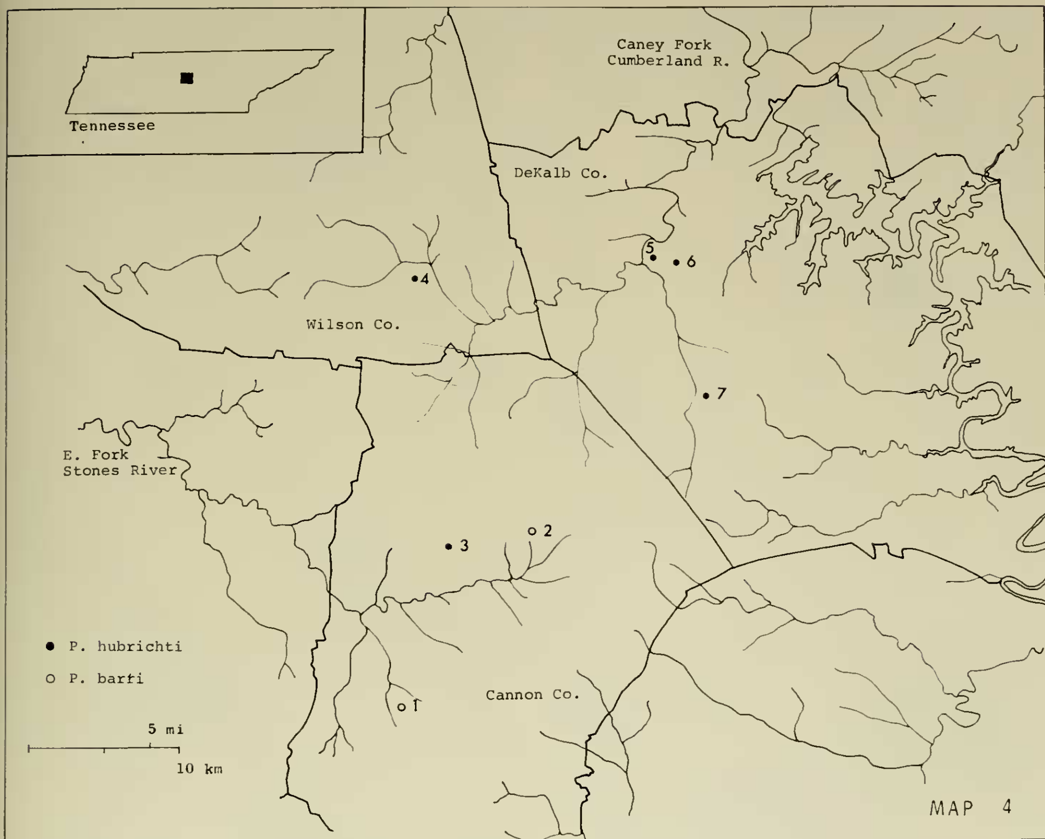
Variation. No variation noted.

Etymology. Named for Dr. Thomas C. Barr, in recognition of his aid to my studies of cave fauna and beetles.

Field notes. In the two caves in which the species has been taken, it has been found in wet gravels along cave streams, by baiting.

Seasonality. Collections have been made in March, July, and August. Teneral adults were found in August. Larvae are not known.

Distribution. Known only from two caves in Ordovician Bigby-Cannon Limestone, in Cannon County, Tennessee, on two tributary branches of the east fork of Stones River (Map 4). I have seen 63 specimens from the following localities:



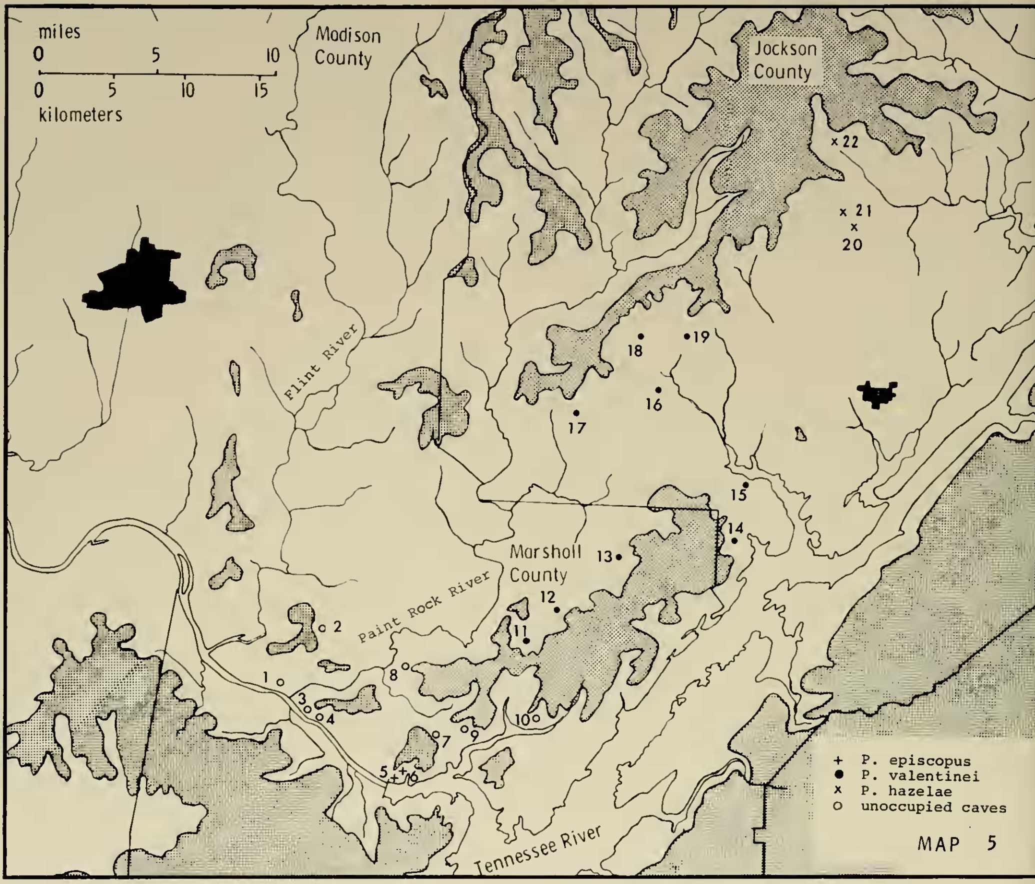
Map 4. Distribution of *Ptomaphagus* (*Adelops*) *hubrichti* (dark circles) and *Ptomaphagus* (*Adelops*) *barri* (open circles), troglobites of caves in central Tennessee. The localities are as follows: 1 Espey Cave, 2 Henpeck Mill Cave, 3 Tenpenney Cave, 4 Hays Cave, 5 Gin Bluff Cave, 6 Avant Cave, 7 Cripps Mill Cave.

TENNESSEE. *Cannon County:* Espey Cave, 6 (SBP, TCB); Henpeck Mill Cave, 57 (SBP).

Distributional comments. The species may be expected in other caves lying between the two known populations, 8 air miles from each other along the eastern flank of Nashville Basin. Several of these other caves (see Barr, 1961a for locations) have been visited but not baited. John Hollins Cave, north of Henpeck Mill Cave, was heavily baited with no success. The nearness of Henpeck Mill Cave, a *barri* locality, to Tenpenny Cave, a *hubrichti* locality, is interesting. They are separated by only two and one-half air miles, with only two minor streams between them as possible dispersal barriers (Map 4). These two species may be found sympatrically in caves to the north. Baiting in Reed Cave, two miles south of Espey Cave, has not produced the beetle. It also has not been found by hand collecting in Davenport Cave. Baiting of this and other Cannon County caves is needed.

Ptomaphagus hazelae new species
Figures 26, 105, 148; Map 5

Holotype male and allotype female in MCZ (no. 31889). Type locality: Alabama, Jackson County, Tumbling Rock Cave. Type data: 3.vii.1969, S. & J. Peck leg. Paratypes: 10 with same data.



Map 5. Distribution of *Ptomaphagus* (*Adelops*) *episcopus*, *valentinei* and *hazelae*, troglobitic species of northeastern Alabama. Stippling as in Map 3. Geology from Malmberg and Sanford (1963) and Adams et al. (1926). The localities are as follows: 1 Clark Bluff Cave, 2 Morring Spring Cave, 3 Merrill Cave, 4 Painted Bluff Cave, 5 Honeycomb Cave, 6 McHardin Cave, 7 Bishop Cave, 8 Keller Cave, 9 Ledbetter Cave, 10 Dunham Cave, 11 Kirkland Cave, 12 Guffey Cave, 13 Cathedral Cave, 14 Mink Cave, 15 Sauta Cave, 16 Larkin Cave, 17 Pig Pen Cave, 18 Schiffman Cove Cave, 19 Limrock Blowing Cave, 20 Ivey Bottom Cave, 21 Driftwood Cave, 22 Tumbling Rock Cave.

Diagnosis. Limited to caves in the headwaters of Mud Creek, Jackson County, Alabama. Similar to *valentinei* but the combination of the elongate thin spermatheca without a crest and the strongly curved aedeagus with an upturned tip serves to distinguish this species from *P. valentinei.*

Description. Length 2.6–3.0 mm. Width 1.2–1.5 mm. Shape oval. Head width, from antennal base to margin across eye, 5.8 times width of eye. Antennae (Fig. 105) flattened, thin and long, reaching into first third of elytra when laid back; segment III clearly longer than II; in profile IV, V, and VI gradually widening and shortening; VII elongate conical; VIII longer than wide. Pronotum sides parallel in hind half; 1.4 times as wide as long; striae on disc present but faint. Elytra 1.5 times as long as wide at base. Mesosternal carina medium height, notch absent or vaguely present. Aedeagus (Fig. 26) strongly bent in lateral view, broad at base, narrowing gradually to apex, tip upturned. Spermatheca (Fig. 148) shaft of medium

thickness, posterior end curved under and opening to left, anterior end without crest.

Variation. No variation noted.

Etymology. The species is named for Mrs. Hazel Jones, in recognition of her help and hospitality during more than two seasons of field work in northern Alabama.

Field notes. Forty-one of the specimens have come from Tumbling Rock Cave where they were baited in moist sections of the cave, or from garbage dumps left by people camping in the cave. Two specimens from Driftwood Cave were on a dead mouse.

Seasonality. Adults have been taken in seven months of the winter and summer seasons. Teneral adults have been taken in January, and larvae in December.

Distribution. Known only from three caves on the edge of the Cumberland Plateau in the headwaters of Mud Creek, Jackson County, Alabama (Map 5). I have seen 47 specimens from the following caves: ALABAMA. *Jackson County:* Driftwood Cave, 4 (SBP); Ivey Bottom Cave, 2 (TCB); Tumbling Rock Cave, 41 (SBP, TCB).

Distributional comments. The species is bounded in a few miles both to the north and southwest along the escarpment by populations of *P. hatchi.* Other caves exist in the region but have not been visited or have not been baited. Consequently, the two species may actually exist in closer proximity than is now known.

Barr (1963) surmised the species to be an allopatric population of *P. loedingi* and suggested that it might have subspecific status.

Ptomaphagus fiskei new species
Figures 27, 84, 106, 149; Map 6

Holotype male and allotype female in MCZ (no. 31890). Type locality: Georgia, Walker County, Mountain Cove Farm Cave. Type data: 20.vi.1967, S. Peck and A. Fiske leg. Paratypes: 91 with same data.

Diagnosis. This is the only troglobitic *Ptomaphagus* known from east of Lookout Mountain in Georgia. It is characterized by the third antennal segment being longer than the second, the sinuous ventral surface of the prominent mesosternal carina, and a spermatheca with a small crest on the anterior end and a knob on the posterior end with a dorsal opening.

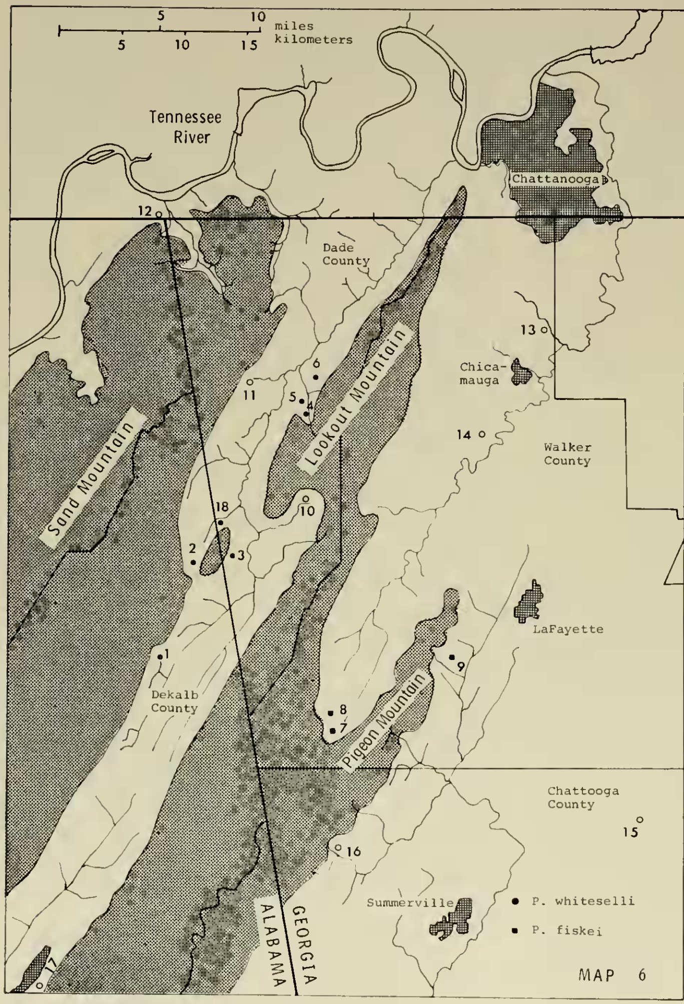
Description. Length 2.8–3.1 mm. Width 1.3–1.5 mm. Shape oval. Head punctured. Width of head across eye from antennal insertion to margin 3.2 times width of eye. Antennae (Fig. 106) elongate, slender, reaching into first 1/4 of elytra when laid back; segment III longer than II; IV, V, and VI sequentially shorter and wider; VII conical; VIII longer than wide; IX and X longer than wide. Pronotum at base 1.4 times as wide as long; widest 1/3 before base; hind margins sinuous; striae absent on disc, faint at margins. Elytra 1.5 times as long as wide at base, slightly wider 1/3 from base. Mesosternal carina (Fig. 84) prominent, ventral margin sinuous; notch absent or only faintly present. Aedeagus (Fig. 27) thin, slightly curved, tapering to tip, tip downcurved. Spermatheca (Fig. 149) with straight shaft; posterior end with knob, opening dorsally; anterior end with hook, bearing small crest.

Variation. No variation noted.

Etymology. Named for Alan Fiske in recognition of his great aid in field work in 1967 and 1968.

Field notes. Taken in all three known localities by baiting. Abundant on damp *Neotoma* rat dung in Mountain Cove Farm Cave. Found in Pettijohn Cave only in the entrance room. Extensive trapping and baiting in Bible Spring Cave took only two specimens in a pile of rocks at the top of a small dome pit, and none along the streams.

Seasonality. Specimens have been collected only in June and July. Larvae were taken in all three localities and tenerals only in Mountain Cove Farm Cave (of the 93 in the type series collected in late June, 13 are teneral).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LaFayette
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7
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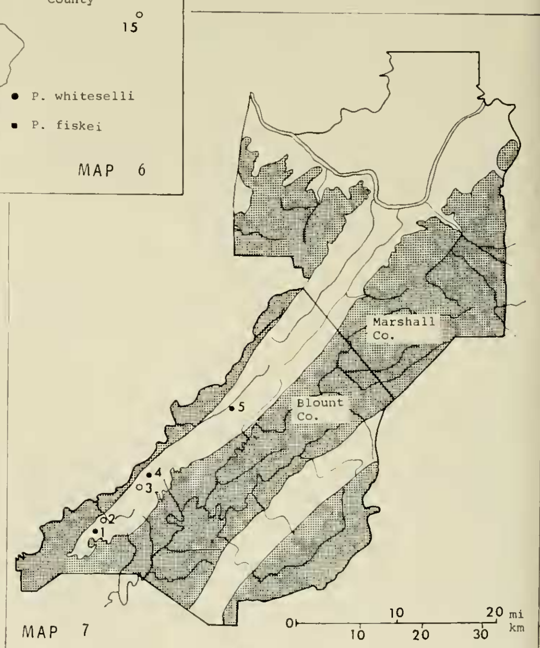
P. whiteselli
P. fiskei
ALABAMA
GEORGIA
17
MAP 6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MAP 7

Distribution. Known only from caves on the east and west flanks of Pigeon Mountain, a spur of Lookout Mountain (Map 6). I have seen 154 specimens from the following 3 localities: GEORGIA. *Walker County:* Bible Spring Cave, 2 (SBP); Mountain Cove Farm Cave, 115 (SBP); Pettijohn Cave, 37 (SBP).

Distributional comments. This species demonstrates how closely the distribution of the troglobitic *Ptomaphagus* is tied to the flat-bedded rocks of the escarpment of the Cumberland Plateau. Baiting in three nearby caves to the east in rocks of the folded and faulted Appalachian Valley yielded no *Ptomaphagus.* Subterranean dispersal into the limestones of these more easterly caves may be limited by the discontinuous nature of the limestones resulting from the folding and faulting in the Appalachian Valley. A prominent fault flanks the eastern scarp of Lookout-Pigeon Mountain, bringing to the surface less cavernous Cambrian Knox dolomites (Butts, 1946).

Extensive baiting in Blowing Spring Cave, about 10 miles to the southwest along the Plateau escarpment, did not yield beetles. Between these points may exist the true southwestern range limit of the species.

Biological survey work has been conducted in other caves in the folded and faulted rocks of the Valley and Ridge Province of northwestern Georgia and eastern Alabama, but has not yielded *Ptomaphagus* (Holsinger and Peck, 1971; Peck, unpublished data). This seems to confirm the observation of the restriction of troglobitic *Ptomaphagus* to the flat-bedded limestones of the Interior and Cumberland plateaus.

Ptomaphagus walteri new species
Figures 28, 85, 107, 150; Map 7

Holotype male and allotype female in MCZ (no. 31891). Type locality: Alabama, Blount County, Bryant Cave. Type data: 19.iii.1966, S. Peck leg. Paratypes: 14 with same data.

Diagnosis. This is the only troglobitic *Ptomaphagus* known from Blount County, Alabama. It is characterized by the prominent mesosternal keel, without a notch; the thin, slightly curved aedeagus; and the spermatheca with both a posterior knob with an opening to the right, and an anterior end with no crest.

Description. Length 2.8–3.0 mm. Width 1.3–1.5 mm. Head punctured; width of head from antennal base to margin across eye 4.1 times as wide as eye. Antennae (Fig. 107) medium length, thin, reaching into first 1/4 of elytra when laid back; segment III longer than II, both shorter than I; IV, V, and VI shorter than II, each sequentially wider; VIII 1 1/2 times as long as wide; VIII twice as wide as long; IX and X subequal, quadrate. Pronotum at base 1.5 times as wide as long; widest 1/3 before

←

Map 6. Distribution of *Ptomaphagus (Adelops) whiteselli* (dark circles) and *Ptomaphagus (Adelops) fiskei* (dark squares), troglobitic species of caves in northeastern Alabama and northwestern Georgia. The open circles are caves in which baiting has attracted no *Ptomaphagus*. Stippling as in Map 3. Geology after Butts (1946). The localities are as follows: 1 Sequoyah Cave, 2 Deerhead Cove Cave, 3 Byers Cave, 4 Case Caverns, 5 Sittons Cave, 6 Morrison Cave, 7 Mt. Cove Farm Cave, 8 Bible Spring Cave, 9 Pettijohn Cave, 10 Johnson Crook Cave, 11 Howards Waterfall Cave, 12 Nickajack Cave, 13 Cave Spring Cave, 14 Horseshoe Cave, 15 Parker Cave, 16 Blowing Spring Cave, 17 Manitou (Ft. Payne) Cave, 18 Twin Snakes Cave.

Map 7. Distribution of *Ptomaphagus (Adelops) walteri*, a troglobite of caves in Blount County, in northcentral Alabama, in the southern end of the Sequatchie Valley. Closed circles indicate known localities, open circles are localities in which baiting has yielded no specimens. Dark stippling (south of Tennessee River only) as in Map 3. Caves occur in the valley in the Bangor Limestone. Limestone is also exposed in Murphree Valley in southeastern Blount County. Topography and geology from Adams et al. (1926). Numbers refer to the following localities: 1 Bryant Cave, 2 Randolf Cave, 3 Catfish Cave, 4 Bangor Cave, 5 Wildcat Cave.

base; hind margin entire; striae on disc absent, faint on margins. Elytra 1.4 times as long as wide at base; slightly wider 1/3 from base. Mesosternal carina (Fig. 85) strong, prominent; ventral surface straight; notch absent. Aedeagus (Fig. 28) almost straight in middle, arcing to ends, narrowing to sharp tip, tip downcurved; setation reduced to two or three on each side of tip; parameres with only two (rarely three) apical setae. Spermatheca (Fig. 150) with slightly curved shaft; knob on posterior end with opening to right; anterior end with hook, no crest on knob.

Variation. No variation noted.

Etymology. Named for Dr. Walter B. Jones, in recognition of his hospitality and encouragement to myself and other students of the cave fauna of Alabama.

Field notes. The type series was taken on human dung on dryish soil a few hundred feet from the entrance of Bryant Cave. The one specimen from Wildcat Cave was found under a rock. The Bangor Cave collections were made by Walter B. Jones in June 1937 and September 1940. I have repeatedly tried to bait specimens from Bangor Cave. The failure may reflect extinction of the Bangor Cave population. The extinction may have resulted from two events. (1) A gaming house and beer hall were at one time operated in the cave. These structures burned in the 1940's, and the fire may have consumed the oxygen in the cave, killing the fauna. (2) The cave environment may have been unfavorably altered with the opening of a back entrance to the cave in the 1950's. The opening, made in a mushroom farming venture, may have altered air flow and soil moisture conditions. However, other cave fauna is now present in the cave; *i.e.*, the troglobitic millipede *Scoterpes*, the troglobitic collembolan *Pseudosinella hirsuta*, and the troglophilic pselaphid beetle *Batriasymmodes spelaeus*.

Seasonality. Adults have been collected only in March, May, and June. Tenerals and larvae are not known.

Distribution. Known from three caves, lying in a straight line along the southern end of the Sequatchie Valley in the Bangor Limestone, in the drainage of the Black Warrior River (Map 7). I have seen 24 specimens from the following three localities: ALABAMA. *Blount County:* Bangor Cave, 7 (UANH), Bryant Cave, 18 (SBP), Wildcat Cave, in southwest Blountsville, 1 (FMNH).

Distributional comments. The straight line range from Wildcat Cave to Bryant Cave is 21 miles. Bryant Cave lies 9 miles to the southwest of Bangor Cave. I have frequently and heavily baited two caves (Randolf and Catfish) between Bryant and Bangor with no success. All these caves, and others not yet collected, are in the Bangor Limestone, which is exposed in an unbroken line on both sides of this southern end of the Sequatchie Valley from a few miles southwest of Blount Springs to the northeast of Guntersville.

The species may exist in other caves to the northeast of Blountsville (Wildcat Cave). The limestones sink below the Pennsylvanian rocks a few miles to the southwest of Bryant Cave (near Rickwood Caverns), so this will mark the limits of the range in this direction.

Ptomaphagus whiteselli Barr
Figures 29, 86, 108, 151; Map 6

Ptomaphagus (*Adelops*) *whiteselli* Barr, 1963: 55. Holotype male, in AMNH, seen. Type locality: Georgia, Dade County, Sittons Cave.

Diagnosis. This is the only troglobitic species known from the caves in Lookout Valley between Sand and Lookout mountains in DeKalb County, Alabama, and Dade County, Georgia. The combination of a very slender and curved aedeagus and a spermatheca with only a slight knob at the posterior end of the straight shaft serves to distinguish this species from others.

Description. Length 2.2–2.6 mm. Width 1.3–1.4 mm. Head punctured; width across head from antennal base across eye to mar-

gin 3.6 times width of eye. Antennae (Fig. 108) medium length, extending to base of pronotum when laid back; segment II and III subequal, shorter than I; IV, V, VI progressively shorter and thicker, VII conical, VIII 3/4 as long as wide; IX longer than X. Pronotum 1.5 times as wide at base as long; widest 1/3 before base; sides behind curving into hind angles; hind margin sinuous; striae on disc fainter than on sides. Elytra 1.4 times as long as wide at base. Mesosternal carina (Fig. 86) high, notch absent. Aedeagus (Fig. 29) slender, slightly curved, gradually tapering to point at tip, tip slightly bent downward. Spermatheca (Fig. 151) shaft straight, posterior end with slight knob, opening to right, anterior end with small hook, crest absent.

Variation. No variation noted.

Field notes. Most of the specimens of the species have been taken by baiting. In Sequoyah Cave the beetles live both in gravels along the stream and in sections appearing to be only slightly moist sand and soil with no obvious food source.

Seasonality. No reproductive seasonality exists in a laboratory culture from Morrison Cave, and none probably exists deep in caves. Adults have been collected only in June, July, August, November, and December. Tenerals are known only from one November collection, and larvae only from one June collection.

Distribution. The species has a straight line range of 15 miles (Map 6) in Lookout Valley between Sand Mountain and Lookout Mountain. I have seen 209 specimens from the following seven localities: ALABAMA. *DeKalb County:* "Cave in Deer Head Cove," 1 (SBP); Sequoyah (Ellis) Cave, 56 (SBP). GEORGIA. *Dade County:* Byers Cave, 105 (SBP); Case Caverns, 3 (SBP); Morrison Cave, 20 (SBP); Sittons Cave, 27 (SBP, TCB); Twin Snakes Cave, 1 (SBP).

Distributional comments. The species occurs in caves on both sides of Lookout Creek, flowing into the Tennessee River, and is apparently restricted to this drainage. The valley and its limestone escarpment sides continue unbroken southward over the low drainage divide into the drainage of Wills Creek which flows into the Coosa River. Though *P. whiteselli* has not dispersed out of the drainage of Lookout Creek, other troglobitic beetles have. The carabid *Pseudanophthalmus alabamae* occurs in both drainages from Sequoyah Cave southwestward 35 miles to caves at Collinsville (personal data).

A lack of similarity in ranges of two other *Pseudanophthalmus* exists when compared to *Pt. whiteselli* (Map 6). *Ps. fulleri* ranges from Byers Cave and Johnson Crook Cave, northward along Lookout Creek, through Howards Waterfall, Sittons, and Morrison caves, to Tennessee Caverns in Hamilton County just over the state border into Tennessee (personal data). It also occurs east of Lookout Mountain in Horseshoe Cave. In contrast, *Pt. whiteselli* is not known as far north as Tennessee Caverns, nor has it been found by baiting in Johnson Crook Cave, or in Horseshoe Cave. *Ps. digitus* also ranges from Tennessee Caverns southwestward to Byers and Johnson Crook caves, but is not known inbetween (personal data, and data in Holsinger and Peck, 1971).

Ptomaphagus valentinei Jeannel
Figures 30, 87, 109, 152; Map 5

Ptomaphagus (*Adelops*) *valentinei* Jeannel, 1933: 252. Type in MNHN, not seen. Type locality: Alabama, Jackson County, Sauta (Old Salter) Cave. Jeannel, 1936: 93.

Ptomaphagus (*Adelops*) *valentinei valentinei* Jeannel, 1949: 103; Barr, 1963: 56.

Diagnosis. This species is distinguished from others in the caves of northeastern Alabama by its parallel hind pronotal margins, vague mesosternal notch, elongate antenna with segment III markedly longer than II, and spermatheca with thin curved central shaft with distinct crest on anterior end and posterior end curving and opening to left.

Description. Length 2.5–3.2 mm. Width

1.3–1.7 mm. Head punctured; width of head from antennal base to margin across eye 5.5 times width of eye. Antennae (Fig. 109) slender, elongate, reaching into anterior third of elytra when laid back; segment III markedly longer than II; IV, V, and VI sequentially decreasing in length and increasing in width; VII conical, VIII longer than wide. Pronotum at base 1.5 times as wide as long, widest at base; sides parallel at base; hind margin slightly sinuous; striae on disc feeble. Elytra at base wider than pronotum at base; 1.5 times as long as wide at base. Mesosternal carina (Fig. 87) medium, notch present but vague. Aedeagus (Fig. 30) thin, only moderately tapered, tip thin and downturned or broad. Spermatheca (Fig. 152) with thin curved central shaft, posterior end with curve, anterior hooked end small with prominent crest.

Variation. The aedeagus is more heavily hooded at the tip in Sauta Cave, and thinner and downcurved at the tip in Limrock Blowing Cave. The shape of the hind femora varies between populations, being more slender in Limrock Blowing Cave. The spermathecal posterior tip opens to the right in a few specimens.

Field notes. Most of the specimens of this species have been collected by baiting. It is abundant on cricket guano in a crawl way at the back of Schiffman Cove Cave. Twenty-seven were taken on a damp, rotting *Neotoma* rat nest in a side passage near the entrance of Limrock Blowing Cave, and on *Neotoma* droppings in Pig Pen Cave.

Seasonality. No seasonality exists for reproduction in this species. A laboratory culture has been maintained of material from Schiffman Cove Cave, and reproduction continues with no seasonal fluctuation. Adults have been taken in seven caves in January, February, March, July, and August. Larvae have been found in five caves in June, July, August, and December.

Distribution. The species is distributed in caves in Mississippian limestone at the edge of the Cumberland Plateau in southern Jackson and northern Marshall counties, Alabama, between the Tennessee and Paint Rock rivers. I have seen 239 specimens from the following nine caves (Map 5): ALABAMA. *Jackson County:* Larkin Cave, 2 (SBP); Limrock Blowing Cave, 34 (SBP, UANH); Mink Cave, 22 (SBP); Pig Pen Cave, 24 (SBP); Sauta (Salter) Cave, 95 (SBP, TCB, UANH); Schiffman Cove Cave, 22 (SBP). *Marshall County:* Cathedral Caverns (Bat Cave), 32 (SBP, TCB, UANH); Guffey Cave, 8 (TCB); Kirkland Cave, 16 (SBP).

Distributional comments. The species may be expected to occur in other caves on the southeastern flanks of Gunter Mountain, and between presently known localities. I did not take *Ptomaphagus* by baiting in Kellers Cave in the western end of Gunter (Grassy) Mountains. Baiting by Dick Graham, and later, myself, did not yield beetles on the southern flank of Gunter Mountain in Dunham Cave. Baiting failure was also met by Graham in Ledbetter Cave, Bishop Cave, Natural Bridge Cave, Walnut Cave, and Freyder Cave.

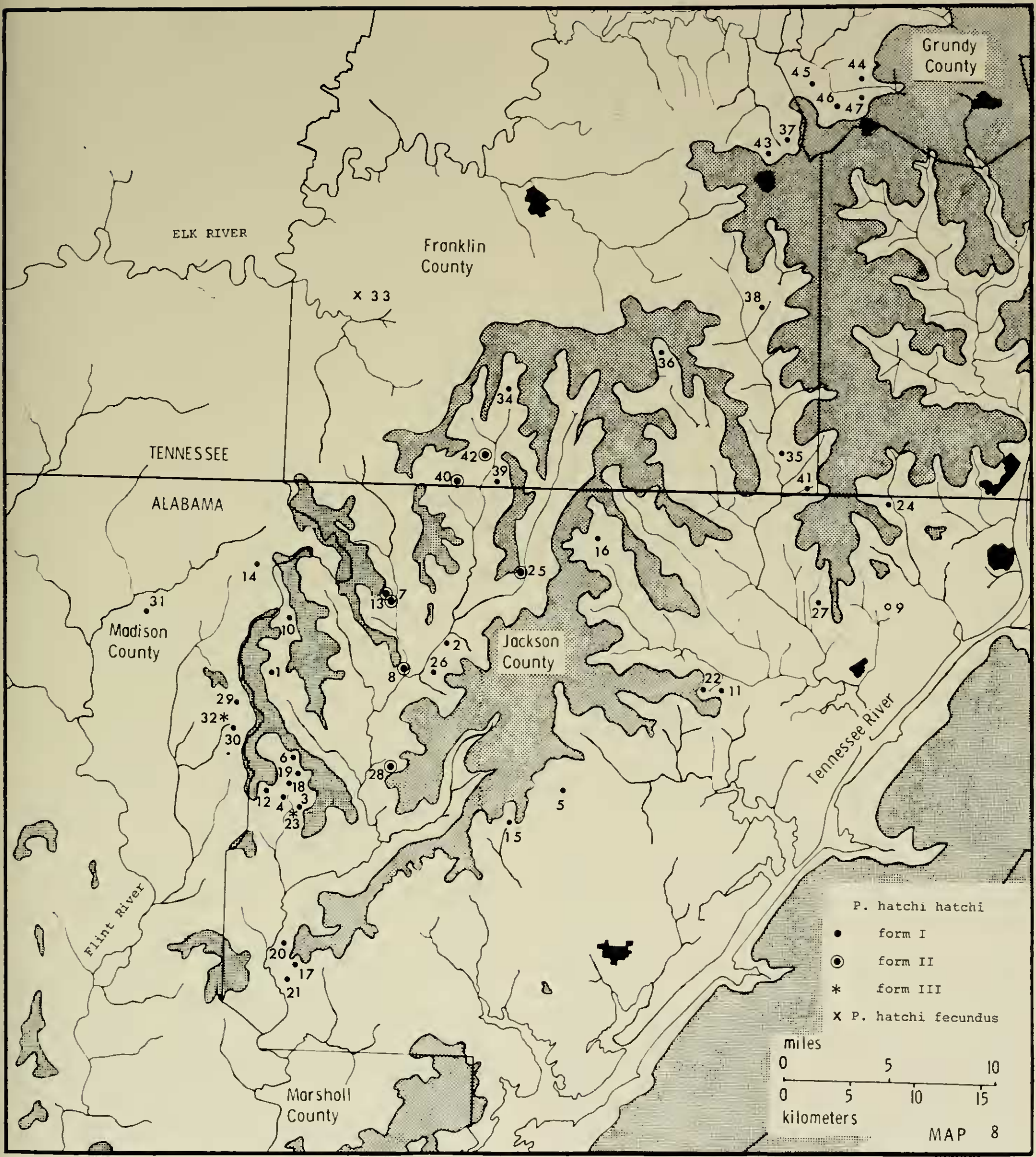
The potential dispersal barrier of the low limestones of Stephen's Gap has been crossed, connecting the Gunter Mountain populations and those three in the southeastern flank of the unnamed mountain running from Woodville to Larkinville. These latter three populations are bounded by populations of *P. hatchi* (form I) to the west and northeast.

Ptomaphagus hatchi hatchi Jeannel
Figures 31, 32, 88, 110, 111, 153–155; Map 8

Ptomaphagus (*Adelops*) *hatchi* Jeannel, 1933: 252. Type, in MNHN, Paris, not seen. Type locality: Tennessee, Grundy County, Wonder Cave. Jeannel, 1936: 93; 1949: 101; Barr, 1963: 54.

Ptomaphagus (*Adelops*) *henroti* Jeannel, 1949: 102. NEW SYNONYM. Co-type in MNHN, Paris, not seen. Type locality: Alabama, Madison County, Aladdin Cave. Barr, 1963: 56.

Ptomaphagus (*Adelops*) *laticornis* Jeannel, 1949:



Map 8. Distribution of *Ptomaphagus* (*Adelops*) *hatchi*, a troglobitic species of northeastern Alabama, and southcentral Tennessee. Stippling as in Map 3. Geology for Madison County from Malmberg and Sanford (1963), and for Alabama from Adams et al. (1926). The localities are as follows: 1 Borderline Cave, 2 Bouldin Cave, 3 Cave Stand Cave, 4 Clemmons Cave, 5 Cornellison #2 Cave, 6 Devils Stairstep Cave and Keels Cave, 7 Doodlebug Pit-Blowing Cave, 8 Doug Green Cave, 9 Edgefield Cave, 10 Hambrick Cave, 11 Happy Hollow Cave, 12 Honey Hollow Saltpeter Cave, 13 Horseshoe Cave, 14 Hurricane Cave, 15 Indian Rocks Cave, 16 Jess Elliott Cave and Tate Cave, 17 Kennamer Cave, 18 McFarland Cave, 19 McFarland Hollow Blowing Cave and McFarland Spring Cave, 20 Morgue Cave, 21 Nat Cave, 22 Rainbow Cave, 23 Rousseau Cave, 24 Russell Cave, 25 "Section 20" Cave, 26 Swaim Cave, 27 Talley Ditch Cave, 28 Williams Saltpeter Cave, 29 Aladdin Cave, 30 Hutton Cave, 31 Jacks Cave, 32 Scott Cave, 33 Caney Hollow Cave, 34 Caroline Cove Cave, 35 Crownover Saltpeter Cave, 36 Custard Hollow Cave, 37 Dry Cave, 38 Lost Cove Cave, 39 Mill Hollow Head Cave, 40 Putnam Spring Cave, 41 Ronnie Willis Cave, 42 Round Mountain Cave, 43 Wet Cave, 44 Crystal Wonder Cave, 45 Partin Spring Cave, 46 Trussell Cave, 47 Wildman Cave.

102. NEW SYNONYM. Type male in MNHN, Paris, seen. Type locality: Alabama, Madison County, Scott Cave. Barr, 1963: 55.

Diagnosis. This is the most variable species of the troglobitic *Ptomaphagus.* It ranges through Grundy and Franklin counties, Tennessee, and Madison and Jackson counties, Alabama. It is distinguished by its smaller size, short antennae which reach into the first quarter of the elytra, the low mesosternal keel with a distinct notch, and the curved hind sides of the pronotum. It is distinguished from *hatchi fecundus* by the characters of the spermatheca.

Description. Length 2.3–2.7 mm. Width 1.2–1.5 mm. Head finely punctured; width of head from antennal base to margin across eye 3.0–4.1 times width of eye. Antennae (Figs. 110, 111) medium, reaching into first quarter of elytra when laid back; segments II and III subequal, to III definitely longer, both shorter than I; IV, V, and VI subequal in length and width, to progressively shortening; VII elongate conical; VIII 3/4 to 1/2 as long as wide; IX longer than X; X quadrate. Pronotum at base 1.4 times as wide as long, sides gradually arcuately narrowing in front; widest 1/3 before base, slightly narrowing behind to base; surface with distinct striae on disc. Elytra at base slightly narrower than prothorax base, widest 1/3 from base; 1.4 times as long as wide. Mesosternal carina medium, notch conspicuous (Fig. 88). Aedeagus (Figs. 31, 32) in profile gradually curved; tip thin to expanded. Spermatheca (Figs. 153–155) of three forms: with fairly straight shaft; anterior end with or without crest; posterior end with or without knob, opening to right, or dorsally.

Variation. There is considerable variation when populations are compared from the extremes of the range (Map 8) of the species. The southwestern populations were formerly recognized as *P. henroti.* But no sharp break in character variation is encountered when a geographic sequence of populations is examined. Previous workers did not have the intermediate populations to work with that I have. Generally, the antennae are less slender, the eyes are smaller, and the hind lateral margins of the pronotum are more curved in the northeastern populations. Larger eye remnants, more slender antennae, and a tendency for parallel hind lateral pronotal margins are found in the southwest around Scott Cave. In the southwest the aedeagus is broader in the base in side view, and the tip is broader in side view in populations in Jacks Cave, Scott Cave, Aladdin Cave, the Morgue Cave, and Hurricane Cave.

The species *laticornis* Jeannel was separated from *henroti,* which inhabits the same cave, solely on the basis of different proportions in the antennal segments. It is synonymized because I believe the type is only a variant individual with slightly shorter and thicker antennal segments.

The spermatheca is clearly polymorphic, with three forms, each having a general geographic distribution. Form I (Fig. 153), without a knob at the distal end, is the most widespread. Form II (Fig. 154) is a very elongate thin spermatheca with a distal twist and large basal crest. This form is found in the following seven caves in the upper Paint Rock River drainage: Round Mountain Cave, Putman Spring Cave, "Section 20" Cave, Horseshoe Cave, Doodlebug Pit-Blowing Cave, Doug Green Cave, and Williams Saltpeter Cave. Form II is allopatrically distributed on both sides of the river, and populations are separated from each other on each side by populations of form I. Form III (Fig. 155), without a basal crest and having a large dorsally opening distal knob, has been found only in Scott and Rousseau Caves in the southwestern end of the species range.

Rather than informally treat the variation in the spermatheca, as I have, another procedure would be to recognize each form as a subspecies or species. I do not believe this is warranted at this time. Each form is without a continuous range. Additional characters that correlate with

the distribution of the spermathecal forms have not been found. Intermediates, indicating hybridization, are not known. The natural test of the species, reproductive isolation in sympatric populations, has not occurred because all populations are allopatric for each form. Only future laboratory breeding studies will determine if intrinsic reproductive barriers have been established. The spermathecal forms may be characters indicating allopatrically distributed sibling species. If greater weight is later given to this character for indicating relationship, form II would be placed as a subspecies of *Pt. valentinei*, or as a species close to *valentinei*.

Field notes. Most of the specimens of this species have been taken by baiting. Large collections were taken on damp *Neotoma* rat dung in Rainbow, Nat, and Mill Hollow Head caves, and in entrance debris and rocks in Jacks Cave. Sixty-two adults were collected from a decaying box turtle where it had fallen in the entrance twilight zone of Horseshoe Cave.

Seasonality. The species probably has no seasonality for populations living deep in caves. I have seen adults taken in every month except October and November. I have seen teneral adults in 12 collections taken in the months of January, February, July, August, September, November, and December. Out of 55 adults taken in August in Talley Ditch Cave, 20 were teneral. Larvae have been taken in six caves in the months of June, July, and August. The beetles may be closer to entrances in the moist spring months, as indicated in Swaim Cave, which yielded beetles to bait in March 1966 but not in July 1967 when the soil was noticeably drier.

Distribution. The species is widely spread in caves in Mississippian limestones at the edge of the Cumberland Plateau, northwest of the Tennessee River and east of the Flint River in Franklin and Grundy counties, Tennessee, and Madison and Jackson counties, Alabama. I have seen 1,487 specimens from the following 45 cave localities (Map 8):

ALABAMA. *Jackson County:* Borderline Cave (no. 830), 3 (SBP); Bouldin Cave (no. 652), 2 (SBP); Cave Stand Cave, 23 (UANH); Clemmons Cave, 4 (UANH); Cornellison Cave no. 2, 45 (SBP); Devils Stairstep Cave, 4 (UANH); Doodlebug Pit-Blowing Cave, 5 (SBP); Doug Green Cave, 44 (SBP); Hambrick Cave, 2 (UANH); Happy Hollow Cave, 44 (SBP); Honey Hollow Saltpeter Cave (no. 74), 38 (UANH); Horseshoe Cave, 62 (SBP); Hurricane Cave, 62 (SBP); Indian Rocks Cave, 89 (SBP); Jess Elliott Cave, 4 (SBP, TCB); Keel Cave, 12 (UANH); Kennamer Cave, 1 (SBP); McFarland Cave, 7 (UANH); McFarland Hollow Blowing Cave (no. 66), 45 (UANH); McFarland Spring Cave, 52 (UANH); Morgue Cave, 8 (SBP); Nat Cave, 11 (SBP); Upper Rainbow Cave, 44 (SBP); Rousseau Cave, 6 (SBP, UANH); Russell Cave (Montague, or Pig entrance), 6 (SBP); "Section 20" Cave, 10 (SBP); Swaim Cave, 22 (SBP); Talley Ditch Cave, 60 (SBP, TCB); Tate Cave, 1 (SBP). *Madison County:* Aladdin Cave, 89 (SBP, TCB, UANH); Hutton Cave, 83 (UANH); Jacks Cave, 51 (SBP, UANH); Scott Cave, 229 (SBP, TCB, UANH). TENNESSEE. *Franklin County:* Caroline Cove Cave, 9 (SBP); Crownover Saltpeter Cave, 19 (TCB); Dry Cave, 22 (TCB); Mill Hollow Head Cave, 37 (SBP); Putman Spring Cave, 45 (SBP); Rannie Willis Cave, 40 (SBP, TCB); Round Mountain Cave, 24 (SBP); Wet Cave, 1 (TCB). *Grundy County:* Crystal Cave, 10 (TCB); Trussell Cave, 2 (TCB); Wildman Cave, 2 (SBP, TCB).

Distributional comments. I have not seen material from Wonder Cave, the type locality, but nearby Crystal Cave is part of the same system and would be inhabited by the same population. Barr (1963) reports the following localities from which I have not seen material: Grundy County, Partin Spring Cave; Franklin County,

Custard Hollow Cave. Jeannel (1949) reports material from Lost Cove Cave, Franklin County, but I have seen none and I found none in August 1968.

Within its range, the beetle may be expected in every cave. When not found by hand collecting, it has been taken by bait in every cave but Edgefield Cave. Other caves in the range have been visited but hand collected only. No extrinsic barriers to dispersal exist to break the subspecies distribution. Continuous limestone suitable for interconnecting subterranean dispersal corridors connects all known populations. However, one notably distinct cluster of populations exists (Map 8), bounded by populations of other species. The Indian Rocks Cave and Cornellison Cave populations are bounded on the east in the same escarpment by *P. hazelae,* and on the southwest by *P. valentinei.* I later suggest that at least part of the complex distributional pattern of spermathecal variation in this subspecies is a result of overland dispersal of already spermathecally differentiated ancestors in Wisconsin time.

The disjunction of the populations of spermathecal forms has been discussed under variation. I have made only a simple analysis of this variation. It is certainly more complex and will reward additional collecting and study.

Ptomaphagus hatchi fecundus Barr
Figures 33, 89, 112, 156; Map 8

Ptomaphagus (Adelops) fecundus Barr, 1963: 57. New Combination.

Holotype male and allotype female in AMNH, seen. Type locality: Tennessee, Franklin County, Caney Hollow Cave.

Diagnosis. Known only from the type locality cave, in the edge of the Central Basin of Tennessee. The subspecies is characterized the same way as *hatchi hatchi,* but separated from it by the shape of the spermatheca.

Description. Similar in all respects to *hatchi hatchi* with the following exceptions: Head width from antennal base to margin across eye 3.5–4.5 times width of eye. Antennae (Fig. 112) with segment III distinctly longer than II; IV, V, and VI progressively shortening; VII elongate conical; VIII twice as wide as long; IX and X slightly longer than wide. Pronotal striae on disc faint or absent, distinct on margins. Mesosternal carina (Fig. 89) lower. Aedeagus (Fig. 33) thinner, tip expanded in side view. Spermatheca (Fig. 156) with sinuous shaft; posterior end bent to left, opening dorsal; anterior end with small hook, distinct crest.

Variation. No variation noted.

Field notes. Barr (1963) reported the beetles to be "so numerous that it was difficult to traverse the cave without stepping on them." They were feeding on bat guano. I visited the cave, but did not bait it, in July and August 1965 and found no beetles. The marked decline in the apparent population density may be connected with the disappearance since 1963 of the bat colony that formerly occupied the cave.

Seasonality. Known only from the single collection of Barr in May 1959.

Distribution. Known only from the type locality (Map 8). I have seen the 94 paratypes.

Distributional comments. The type cave lies in the limestones of the Catheys formation exposed in the margin of the Central Basin and Highland Rim of Tennessee. It is only four air miles from Caney Hollow Cave to the limestones of the escarpment of the Cumberland Plateau, inhabited by *hatchi hatchi.* However, these two limestones are separated by the noncavernous Chattanooga Shale. This geologic horizon must act as a barrier to subterranean dispersal and gene flow between the beetle populations.

There are no known nearby caves in the Catheys Formation. The subspecies may well be limited to Caney Hollow Cave.

Ptomaphagus episcopus new species
Figures 34, 90, 113, 157; Map 5

Holotype male and allotype female in MCZ (no. 31892). Type locality: Alabama, Marshall County, McHardin Cave. Type data: 14.viii.1967, S. Peck and A. Fiske leg. Paratypes: two with same data, and two from same locality, 3.xii.1967, R. Graham leg; 35 from Honeycomb Cave, Marshall Co., 24.i.1939, W. B. Jones.

Diagnosis. The species is known only from caves in Bishop Mountain, Marshall County, Alabama. It is most similar to *P. hatchi.* The combination of the low mesosternal carina with a notch, the stout aedeagus, and the posterior end of the spermatheca without a knob serve to characterize the species.

Description. Length 2.5–2.9 mm. Width 1.3–1.6 mm. Head punctured; width of head from antennal base to margin across eye 4.7 times width of eye. Antennae (Fig. 113) medium length, reaching first 1/4 of elytra when laid back; segments II and III subequal, to III distinctly longer than II, both shorter than I; IV, V, and VI subequal; VII elongate conical; VIII 3/4 as long as wide; IX and X slightly longer than wide. Pronotum at base 1.4 times as wide as long; widest 1/3 before base; hind margin slightly sinuous; striae faintly present on disc. Elytra 1.5 times as long as wide at base. Mesosternal carina (Fig. 90) low, notch distinct to faint. Aedeagus (Fig. 34) stout, gently arcing; distinct crest on tip. Spermatheca (Fig. 157) with curved shaft, posterior end undulating to dorsally facing opening, tiny crest on anterior end.

Variation. Some variation exists in the posterior end of the spermatheca, and the shape of the hind femora. The McHardin Cave specimens are larger than those from Honeycomb Cave, and have antennal segment III distinctly longer than II.

Etymology. Latin, *episcopus*, bishop, a noun in apposition, referring to Bishop Mountain in which the species is probably limited.

Field notes. The six type specimens were taken with liver bait, under a large rock at the back of McHardin Cave, about 20 meters from the entrance. The Honeycomb Cave specimens were collected in January 1939 by Walter B. Jones, who collected 120 specimens, and reports (personal communication) they were so abundant that several hundred more could have been collected. Honeycomb Cave is now mostly flooded by the impoundment of the Tennessee River, behind Guntersville Dam. An upper entrance still exists to the cave, which I visited in 1968. From the Tennessee River there is free circulation of warm river water into the cave, which raises the cave air temperature. Normal cave temperature in Jackson County, Alabama is 15°C. In late August, Honeycomb Cave was 25°C near the ceiling, with a water temperature of 27°C. Soil in the side chamber was 22°C. Baiting did not yield *Ptomaphagus*, but other beetles (the carabids *Agonum caudatum* and *Tachys*) were unusually abundant for an Alabama cave. The warm conditions may have exterminated most of the cave-adapted fauna. One specimen of the troglobitic millipede *Tetracion* was collected, so all the cave-adapted fauna is not yet gone.

Seasonality. The species has been collected in January, August, and December. Tenerals and larvae are not known.

Distribution. The species is known only from two caves in Bishop Mountain (Map 5). I have seen 41 specimens from the following two localities: ALABAMA. *Marshall County:* Honeycomb Cave, 35 (UANH); McHardin Cave, 6 (SBP).

Distributional comments. Baiting did not take the species in Bishop Cave, on the north slopes of Bishop Mountain. Nearby Hambrick Cave in Honey Bluff is now the home of a large *Myotis sodalis* bat colony. It may now be as unsuitable as Honeycomb Cave as a beetle habitat because it too is warmed by circulating waters of the Tennessee River.

The species may have crossed from

Bishop Mountain through limestones under low Ricketts Gap into the Grassy Mountain to the northeast. Caves exist there, and some have been collected, but have not been baited. Dispersal may be also possible to the west of Bishop Mountain, under the low valley to Russell Ridge and Merrill Mountain. Merrill and Painted Bluff Caves in Merrill Mountain have been unsuccessfully baited.

Across the Paint Rock River to the northwest of Merrill Mountain are the contiguous Mayo, Lemley, McKinney, and Meeks mountains in Madison County. *Ptomaphagus* are not known here. The Paint Rock River may have prevented dispersal to them from the east, and the Flint River may have prevented dispersal from the west. Baiting in these mountains in Morring Spring Cave and Clark Bluff Cave took no *Ptomaphagus* but did take *Tetracion*, showing that this large troglobitic millipede was able to disperse into the caves here, but from which direction is not known.

Ptomaphagus hirtus Tellkampf
Figures 2, 6, 35, 36, 91, 114, 158–161; Map 9

Adelops hirtus Tellkampf, 1844: 313, fig. 106. Type: location unknown. Type locality: Kentucky, Edmonson County, Mammoth Cave. Packard, 1871: 745 (record); 1874: 563 (larva); 1876: 283 (ecology and larva); 1888: 78 (biology and pupa). Jeannel, 1922: 90; 1931: 408 (systematics and larva). Hatch, 1933: 210 (systematics, records). Hubbard, 1880: 80 (ecology).

Ptomaphagus (*Adelops*) *hirtus* Jeannel, 1936: 93, figs. 154–155 (systematics); 1949: 99. Barr, 1962: 282 (biology); 1963: 53; 1967c (ecology and distribution).

Diagnosis. This is the only blind cave *Ptomaphagus* in the Mammoth Cave area of Kentucky.

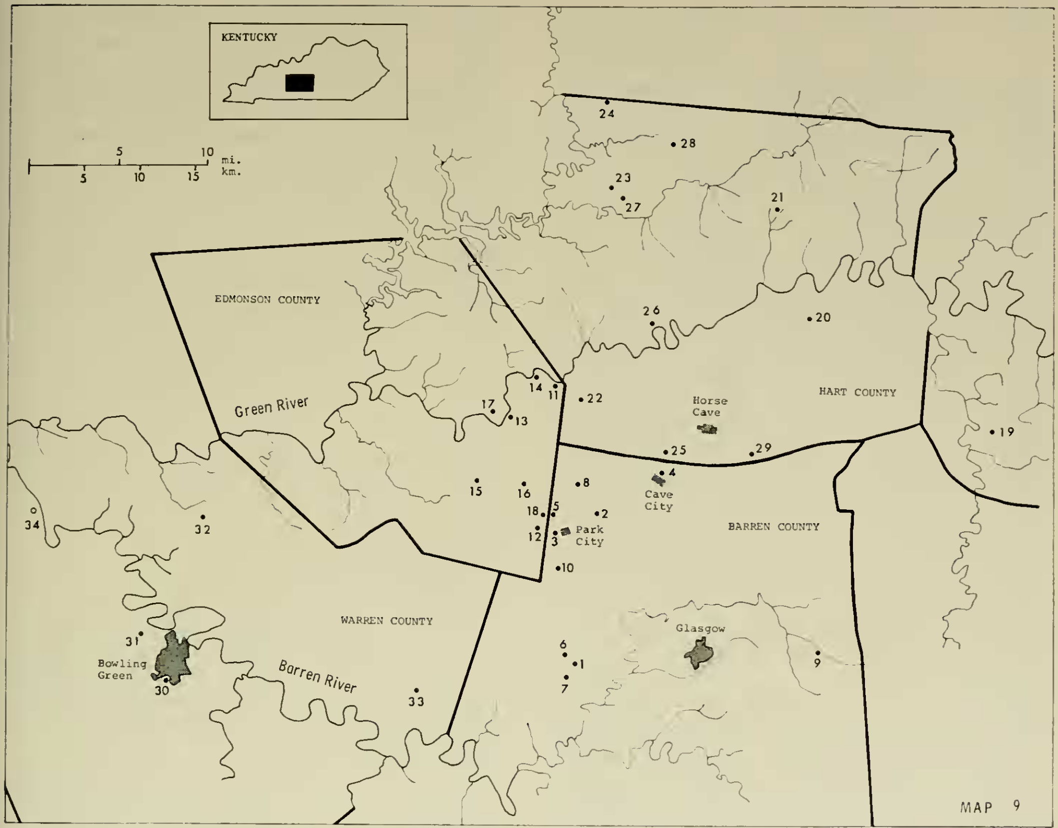
Description. Length 2.0–2.8 mm. Width 1.2–1.4 mm. Head smooth; width of head from antennal base to margin across eye 3.8 times width of eye. Antennae (Fig. 114) medium length, reaching beyond margin of pronotum when laid back; segments II and III, and IV–VI subequal, width uniform; VII elongate, cylindrical; VIII transverse, IX longer than wide, X quadrate, XI longer than wide. Pronotum at base 1.4 times as wide as long; sides arcuately narrowing in front, front angles rounded, widest 1/3 from base, arcuately narrowing behind to hind angles; surface smooth, only traces of striae at margins. Elytra at base slightly narrower than prothorax base, gradually narrowing apically. Mesosternal carina (Fig. 91) strong and prominent. Aedeagus (Fig. 35) in profile straight and thin, fairly uniform width, tip downcurved, narrowing gradually to tip in dorsal view (Fig. 36). Spermatheca (Figs. 158–161) with a slightly curved central shaft, a knob on posterior end with an apical depression and a hooked, curved knob on anterior end.

Variation. The only variation within the species that has been noticed is that of the female spermatheca. Figures 158–161 demonstrate the spermatheca from the center of the range and three extreme populations. The western population (Bypass Cave) has a more stout central shaft. The anterior end is of different proportions in all populations.

Field notes. The ease of collecting the species by baiting with decaying organic material has led to the abundant representation of it in collections at many museums. Barr (1962) reports that guano of the cave cricket *Hadenoecus subterraneus* may be the normal food of the beetle. I have seen them on cricket guano in the Frozen Niagara section of Mammoth Cave, and in Proctor, Whites, and Great Onyx caves. Barr (1962) gives various localities for the beetle in Mammoth Cave.

Seasonality. I have seen specimens collected in every month but January. In the laboratory, reproduction takes place throughout the year.

Distribution. The species is limited to Hart, Edmonson, Barren, and Warren counties, Kentucky. It is known from 41



Map 9. Distribution of *Ptomaphagus* (*Adelops*) *hirtus*, a troglobitic species of central Kentucky. The closed dots represent known localities, and are as follows: 1 Beckton Cave, 2 Brushy Knob Cave, 3 Burnett Cave, 4 Cave City Cave, 5 Diamond Caverns, 6 Duval Saltpeter Cave, 7 Edmunds Cave, 8 Indian Cave, 9 Slick Rock Cave, 10 Walnut Hill Cave, 11 Buzzard Cave, Cathedral Cave and Collins Crystal Cave, 12 Coach Cave and James Cave, 13 Dixon Cave, Mammoth Cave and Whites Cave, 14 Great Onyx Cave, 15 Martins Cave, 16 Proctor Cave, 17 Running Branch Cave, 18 Short Cave, 19 Wisdom Cave, 20 Bald Knob Cave, 21 Barnes Smith Cave, 22 "Cave," 23 Chattlin Cave and Coach Webb Cave, 24 Copelin Cave, 25 Hogan Cave and Ronalds Cave, 26 Logsdon Valley Cave, 27 Puckett Cave, 28 Saltpeter Cave, 29 Bear Wallow Cave, 30 Bypass Cave, 31 Horseshoe Cave, 32 Pruett Saltpeter Cave, 33 Gorman Cave, 34 Thomas Cave.

caves in Mississippian limestones in the western Pennyroyal Plateau, and the Dripping Springs Escarpment, both north and south of the Green and Barren rivers (Map 9). I have seen 861 specimens from the following 41 locations:

KENTUCKY. *Barren County:* Beckton (Tarbarrel) Cave, 3 (TCB); Brushy Knob Cave, 2 (TCB); Burnett Cave, 3 (TCB); Cave City Cave (Railroad Cave), 7 (CAS, TCB, FMNH); Diamond Caverns, 1 (SBP); Duval Saltpeter Cave, 4 (TCB); Edmunds Cave, 47 (SBP, TCB); Indian Cave, 5 (SBP); Lyon Cave (Cave City), 49 (USNM); Slick Rock Cave, 22 (TCB); Walnut Hill Cave, 2 (TCB). *Edmonson County:* Buzzard Cave, 23 (TCB); Cathedral Cave, 1 (SBP); Coach Cave (=Hundred Domes Cave), 5 (TCB, SBP); Collins Crystal Cave, 52 (TCB); Dixon Cave, 20 (CAS, MCZ, TCB, UANH); Great Onyx Cave, 10 (SBP, TCB); James Cave, 20 (TCB); Mammoth Cave, 294 (CAS, AMNH, MCZ, FMNH, TCB,

USNM;) Martins Cave, 1 (TCB); Proctor Cave, 5 (SBP, TCB); Running Branch Cave, 20 (SBP, TCB); Short Cave, 2 (TCB); Whites Cave, 29 (MCZ, SBP, TCB, USNM, UANH). *Green County:* Wisdom Cave, 86 (SBP, TCB). *Hart County:* Bald Knob Cave, 7 (TCB); Barnes Smith Cave, 15 (SBP); "Cave" 2 miles SW Northtown, 14 (TCB); Chattlin Cave, 2 (TCB); Cooch Webb Cave, 5 (TCB); Copelin Cave, 15 (TCB); Hogan Cave, 10 (TCB); Logsdon Valley Cave, 2 (TCB); Puckett Cave, 3 (TCB); Ronalds Cave, 9 (TCB, USNM); Saltpeter Cave, 1 (TCB); Webb Cave, 4 (TCB). *Warren County:* Bypass Cave, 7 (TCB, SBP); Horseshoe Cave, 1 (TCB); Pruett Saltpeter Cave, 57 (SBP); Garman Cave, 1 (SBP).

Distributional comments. It is interesting to note that the Barren and Green rivers have not acted as barriers to dispersal of this species. The maximum extent of the known range is a 55-mile long line from Bypass Cave to Wisdom Cave. Insufficient information exists to answer the question of whether the species has migrated across the rivers, or around the headwaters to inhabit caves on opposite sides of the drainages. I later suggest that the rivers were crossed by individuals dispersing overland in Wisconsin time. A careful study of variation may help answer this question.

The limits of the species range may be partly due to geological conditions. The species does not penetrate deeply the region of the Salem and Warsaw limestones to the east. The northern boundary is considerably beyond the Pennsylvanian river channel crossing northern Hart County, just north of Munfordville. The southwestern limit, lying on the Pennyroyal Plateau of continuous limestones, offers no explanations. Other species of the "Mammoth Cave faunal province" extend farther in this direction than does *P. hirtus*. See Barr (1967c) for a more complete discussion of this zoogeographic province.

Various collections contain specimens from localities that are not now identifiable. These localities, such as the "Lyon Cave" of Packard (1888), are not listed. They are all undoubtedly in the vicinity of Mammoth Cave, and not of importance in gaining a full picture of the range of the species.

Jeannel (1931) reports on a collection from Hidden River Cave, in the town of Horse Cave. I have twice visited the cave but have not found *Ptomaphagus*. Serious pollution of the cave stream resulted in a noticeable deficiency of oxygen in the cave when visited in September 1967. This may have altered the terrestrial cave community.

Extensive baiting did not yield the species in Thomas Cave, Warren County.

Ptomaphagus nicholasi Barr
Figures 37, 115, 162; Map 2

Ptomaphagus (*Adelops*) *nicholasi* Barr, 1963: 53. Holotype male and allotype female in AMNH. Type locality and data: Illinois, Monroe County. Fogelpole Cave, 22.x.1961, Bro. G. Nicholas leg. Three paratypes, same data (TCB). I have seen all specimens.

Diagnosis. This is the only blind cave *Ptomaphagus* known from Illinois. Virtually identical in morphology to *P. hirtus*. The key characters of Barr (1963) do not clearly separate the species from *P. hirtus* when the range of *hirtus* variation is seen.

Description. Length 2.3–2.7 mm. Similar to *P. hirtus* in all features except the following: antennae (Fig. 115) with segments slightly more elongate than in *P. hirtus;* segment VIII about 1/2 as long as wide. Aedeagus (Fig. 37) like that of *P. hirtus*, more slender, tip slightly less deflexed than in *hirtus*. Spermatheca (Fig. 162) like that of *hirtus*, most similar to populations in center of *hirtus* range.

Field notes. The type series was found under a rock at edge of stream in type locality cave (personal communication with Rev. P. Wightman of Bellville, Illinois, who was present at time of collection of the type series).

Seasonality. Known only from the Oc-

tober 1961 collection. Two specimens are teneral.

Distribution. Known only from the type locality (Map 2).

Distributional comments. If this species still is extant, it is exceptionally secretive, or rare. I have extensively baited and trapped in the type locality cave, and in over 15 other caves in Monroe County, Illinois, in summer and winter seasons, for several years, with no success. Cave locations are in Bretz and Harris, 1961.

Ptomaphagus hubrichti Barr
Figures 38, 116, 163; Map 4

Ptomaphagus (*Adelops*) *hubrichti* Barr, 1958: 170. Holotype male and allotype female, in AMNH, seen. Type locality: Tennessee, DeKalb County. Cripps Mill Cave. Barr, 1963: 56.

Diagnosis. It is distinguished from other members of the *hirtus* group by the pronotum being widest at its base. It is one of two blind species inhabiting caves in central Tennessee. The straight aedeagus of the male and more curved spermatheca serve to distinguish it from *P. barri*, the other central Tennessee cave species.

Description. Length 2.6–3.3 mm. Width 1.3–1.4. Head finely punctate. Antennae (Fig. 116) slender, reaching first 1/3 of elytra when laid back; segments II and III, and IV–VI subequal, width uniform; VII large, conical, half as wide as long; VIII wider than long. Pronotum at base 1.6 times as wide as long; widest 1/4 before base, tapering only slightly to hind angles; sides arcuately narrowing to rounded front angles; surface faintly striate at margins. Elytra at base subequal to pronotum, gradually narrowing apically; 1.3 times as long as wide at base. Mesosternal carina strong and prominent. Aedeagus (Fig. 38) very slightly curved in profile, widest in basal third, tip slender and downcurved. Spermatheca (Fig. 163) central shaft curved; posterior end with knob; anterior end with hooked bulge.

Variation. The hind angles of the pronotum are less rectangular in the Tenpenny Cave population. No other variation has been noticed.

Field notes. P. hubrichti is found in very damp situations in the caves. Barr (1958) reports it in wet places, under rocks, on raccoon dung, and on a dead bat. The type locality is not now available for collecting because the waters of the cave feed a fish farm whose owners have closed the cave. The closing is to prevent possible pollution of the cave stream by visitors to the cave. I took 20 specimens in a small hole in silt in Hayes Cave, under a *Ceuthophilus* roost.

Seasonality. Adults have been collected in winter and summer, with tenerals in August. Larvae have been taken in two caves in August.

Distribution. The species is limited to caves in the eastern edge of the Nashville Basin in Ordovician limestones in Cannon, DeKalb, and Wilson counties, Tennessee (Map 4). I have seen 77 specimens from the following localities: TENNESSEE. *Cannon County:* Tenpenny Cave, 7 (SBP). *DeKalb County:* Avant Cave (Lindsay Williams Cave), 3 (TCB, FMNH, UANH); Cripps Mill Cave, 29 (TCB); Gin Bluff Cave, 9 (TCB). *Wilson County:* Hayes Cave, 29 (TCB, SBP).

Distributional comments. The species may be expected in other caves. Baiting has not yielded it in two caves near caves known to contain populations (Reed Cave and John Hollis Cave). Baiting is needed in other Cannon, DeKalb, and Wilson County caves.

The *Consobrinus* Group

Diagnosis. Spermatheca shaped like reversed "S," the anterior and posterior ends either narrow or wide and flattened (Figs. 164–186).

Description. Shape elongate oval. Color light to dark (piceous) brown. Eyes large or partially reduced, pigmented (Fig. 4). Antennae medium or short, long in *giaquintoi.* Pronotum with hind angles faintly acute, discal striae distinct, normally

about 10 striae per 0.25 mm, finer and more closely spaced in *schwarzi* and some populations of *nevadicus* with about 13 per 0.25 mm. Elytra with striae normally about 7 per 0.25 mm and oblique to suture, finer with about 10 per 0.25 mm and transverse to suture in *schwarzi* and some *nevadicus*. Wings fully developed in all species except *cocytus*. Mesosternal carina low except in *giaquintoi*. Legs normal. Aedeagus long, thin, and curved, to short and fairly straight, tip blunt or sharp.

The group contains a total of ten species, collectively distributed from southern Canada and throughout the United States southward to a few populations of species ranging into western Mexico, and with one species limited to eastern Guatemala. One species each from Arizona and Guatemala are troglobites. The others are free living or nest and burrow inhabitants.

Ptomaphagus fisus Horn
Figures 15, 41, 42, 118, 165–170, 200; Maps 10, 13

Ptomaphagus fisus Horn, 1885: 137. Lectotype here designated as male in ANSP (no. 2996), seen. Type locality: Arizona. Hatch, 1933: 204.

Ptomaphagus (*Adelops*) *fisus*, Jeannel, 1936: 91; 1949: 97.

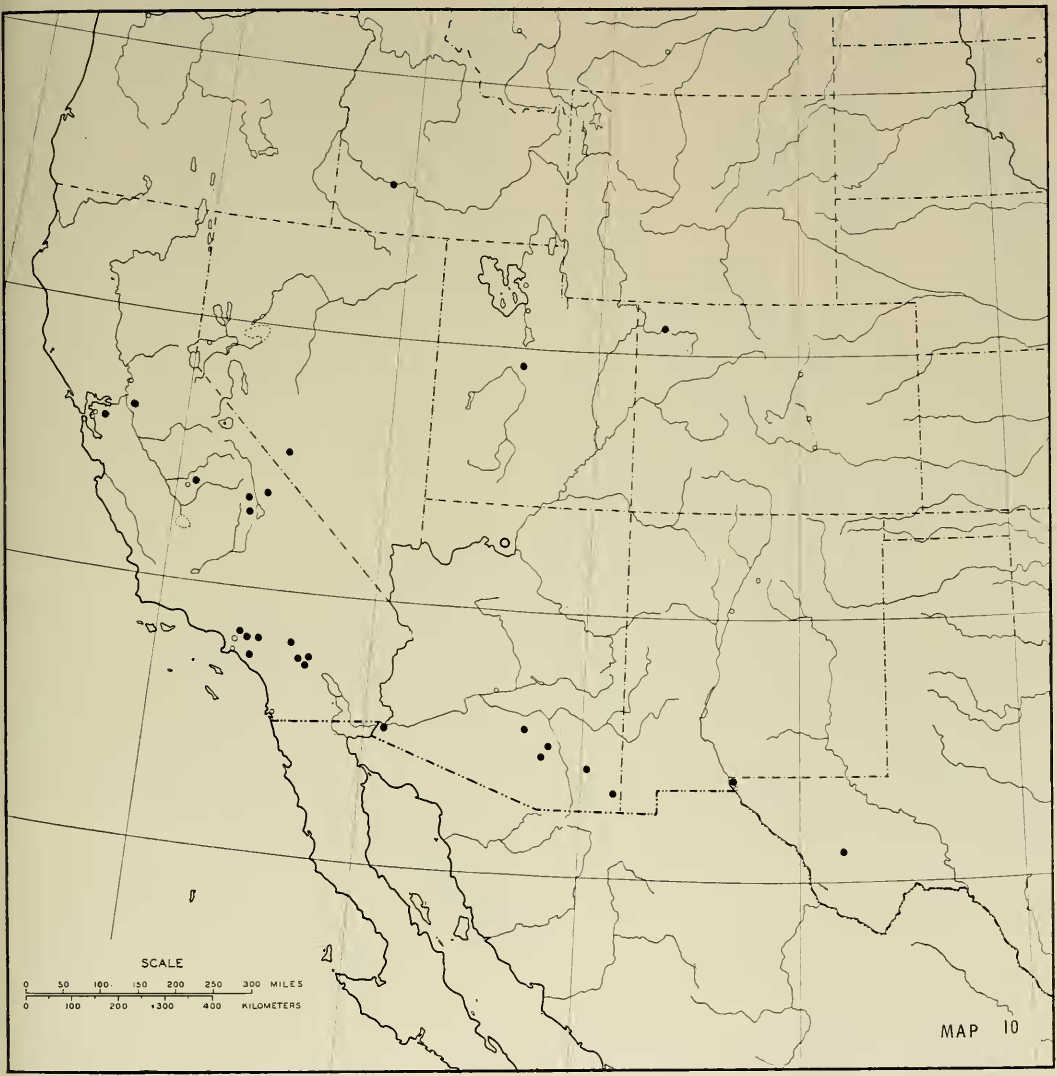
Ptomaphagus (*Adelops*) *inermis* Jeannel, 1933: 251. NEW SYNONYMY. Holotype male in British Museum (Nat. Hist.), Fry Colln., seen. Type locality: "Mexico." Jeannel, 1936: 92.

Diagnosis. The species is widely distributed in the xeric United States from the Rocky Mountain states westward, and south into Mexico. It is distinguished from all others by the female spermatheca, and by the male aedeagus and genital segment. Most males also possess a tooth on the metafemur, a character otherwise found only in *cocytus*.

Description. Length 2.4–2.7 mm. Width 1.1–1.4 mm. Color light to medium reddish brown, head darker, appendages lighter. Head finely punctured. Eyes large, normal; their horizontal diameter 2.7 times width of space between anterior margin and antennal socket. Antennae (Fig. 118) short, not reaching edge of pronotum when laid back; segments II–V longer than wide, VI–X wider than long. Pronotum widest at base, 1.4 times as wide as long; sides gradually widening. Elytra 1.6 times as long as wide at base; male apex rounded transversely truncate; female apex truncate; weakly oblique to suture. Mesosternal notch low, as in *consobrinus* (Fig. 94). Legs with male metafemur with low, broad tooth near middle of posterior margin (Fig. 15) in most populations. Aedeagus (Fig. 41) thin, curved, narrowing gradually to sharp tip; tip in dorsal view (Fig. 42) bluntly to sharply pointed. Genital plates not anteriorly projected, enclosing over 3/4 of medium spiculum gastrale (Fig. 200). Spermatheca (Figs. 165–170) shaft curved; posterior end not broad or flattened, with small crest; anterior end widened, slightly flattened.

Variation. Variation is noted most in the male metafemur and the spermatheca. The metafemoral tooth is present but indistinct in the Colorado specimens, and absent in the male serving as the type of *P. inermis* Jeannel. The spermatheca varies in size and proportion throughout the range, but maintains its distinctive features (Figs. 165–170). The antennal and elytral differences cited by Jeannel for *inermis* do not separate the Mexican material from *fisus* populations. The type of *inermis* has an aedeagal tip sharper than that in Figure 42. The doubtful record from Chihuahua is missing both antennae and spermatheca. Its elytral apex is more drawn out, with a sharper sutural angle than in other observed females.

Field notes. The species was reported by Hubbard (1901) as an inhabitant of ground squirrel and kangaroo rat nests at Palm Springs, California. They were most abundant in nests made of grass near the surface, and not in nests deep in the burrows (at depths up to 8 feet). They have since been taken in kangaroo rat



Map 10. Distribution of *Ptomaphagus* (*Adelops*) *cocytus* (open circle in northcentral Arizona), a troglobite from Grand Canyon, Arizona, and *Ptomaphagus* (*Adelops*) *fisus* (dark dots).

(*Dipodomys*) burrows at Cathedral City, California; in ground squirrel burrows (*Citellus*) in Orange County, California; and in prairie dog burrows in Colorado. A series of 24 was taken under a stone at Palm Springs, and one under a stone and one in a grass pile at Claremont, California.

Seasonality. The species has most commonly been taken in the winter and spring months from October to May. Only two specimens come from outside this period (from Tucson in August). That they have not been taken in the hot summer months from June to September may reflect inactivity of collectors. Larvae are unknown.

Distribution. The species ranges through the xeric regions of the western and southwestern United States from southern Cali-

fornia eastward to west Texas, north to southern Idaho (Map 10) and south into Mexico. I have seen 127 specimens from the following localities:

MEXICO. Locality unknown; Truqui leg., 1 male, 1 female (BMNH, Fry Colln.). The male, the type of *P. inermis*, and the female arrived back at the BMNH in fragments, broken in shipment, according to Mr. P. M. Hammond. Doubtful record: Chihuahua, Majalca Road, 5500′ elev., 30 mi. NW Chihuahua, 14–17.iv.1961, Howden & Martin, 1 damaged female (CNCI). **UNITED STATES.** ARIZONA. *Cochise County:* Apache, 1 (FMNH); Dragoon, 1 (CAS). *Pima County:* Santa Catalina Mts., 2 (CAS); Tucson, 8 (USNM, CAS). *Pinal County:* Picacho, 1 (CAS). *Yuma County:* Yuma, 2 (USNM, INHS). *Unknown state localities:* Catal Springs, 1 (USNM); Galiuro Mt., 1 (USNM); Pinal Mts., 1 (USNM). CALIFORNIA. *Contra Costa County:* Russellman Park (Mt. Diablo), 2 (CAS). *Fresno County:* Lanes Bridge, 1 (CNCI). *Inyo County:* Owens Lake, 5 (CNCI, MCZ); Saline Valley (freshwater spring 1500′ above valley floor on SW slope), 5 (CAS); Goodale Creek (N of Lone Pine), 1 (CAS); No locality, 1 (CNCI). *Los Angeles County:* Azusa, 14 (CAS, MCZ, USNM); Claremont, 2 (INHS); Pasadena, 1 (MCZ). *Orange County:* Santa Ana Canyon, 2 (USNM). *Riverside County:* Cathedral City, 1 (CAS); Palm Springs, 53 (CAS, USNM); Thousand Palms, 1 (CNCI); Pine Springs Ranch (5 mi. E Idyllwild), 1 from malt trap (GHNC). *San Bernardino County:* Kelso Dunes, 1 (CAS); San Bernardino Valley, 1 (MCZ). *San Joaquin County:* Stockton, 4 (CAS). COLORADO. *Moffat County:* Maybelle (prairie dog burrow), 5 (CNCI). IDAHO. *Elmore County:* Glenns Ferry, 1 (USNM). NEVADA. *Esmeralda County:* No locality, 1 (CNCI). TEXAS. *El Paso County:* El Paso, 2 (MCZ). *Jeff Davis County:* Ft. Davis, 1 (MCZ). UTAH. *Juab County:* Levan, 1 (CAS).

Distributional comments. Jeannel (1933) gave the type locality of *P. inermis* Jeannel as Iruqui, Mexico. This was a misinterpretation of the label bearing the collectors name, Truqui, who may have taken the specimens in the vicinity of Guadalajara or Morelia. An exact location probably cannot be determined.

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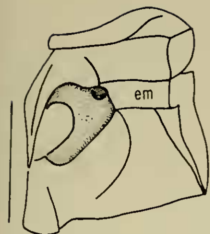
Figures 9–24. Figs. 9–10, left lateral view of thorax; Figs. 11–16, legs; Figs. 17–24, aedeagi. Scale line in lower right 0.5 mm for lateral view of *Ptomaphagus aedeagi*, 0.3 mm for *Ptomaphagus aedeagus* tip. Fig. 9, *Proptomaphaginus puertoricensis*, meso- and metathorax, scale 0.5 mm. Fig. 10, *Ptomaphagus consobrinus*, Torreya Park, Florida, meso- and metathorax, em = mesepimeron, scale 9.5 mm. Fig. 11, *Proptomaphaginus puertoricensis*, male protibia and protarsus, scale 0.2 mm. Fig. 12, *Proptomaphaginus puertoricensis*, female protarsus, scale as in 11. Fig. 13, *Ptomaphagus consobrinus*, Torreya Park, Florida, female protarsus, scale line 0.2 mm. Fig. 14, *P. consobrinus*, Torreya Park, Florida, male protibia and protarsus, scale as in 13. Fig. 15, *P. fisus*, "Ariz., paratype 2996," male metafemur. Fig. 16, *P. cocytus*, paratype, Grand Canyon National Park, Arizona, male metafemur. Fig. 17, *Adelopsis mitchellensis*, Mt. Mitchell, N. Carolina, lateral view aedeagus. Fig. 18, same as 17, dorsal view aedeagus tip, same scale as 17. Fig. 19, *Ptomaphagus shapardi*, Dresser Cave, Oklahoma. Fig. 20, same as 19. Fig. 21, *P. loedingi loedingi*, Pitts Cave, Alabama. Fig. 22. *P. loedingi longicornis*, Crossing Cave, Alabama. Fig. 23, *P. loedingi julius*, House of Happiness Cave, Alabama. Fig. 24, *P. loedingi solanum*, Sheldons Cave, Alabama.



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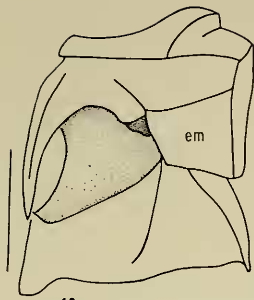

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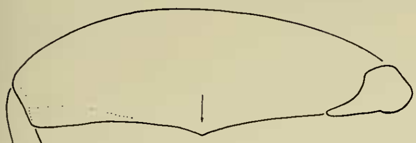

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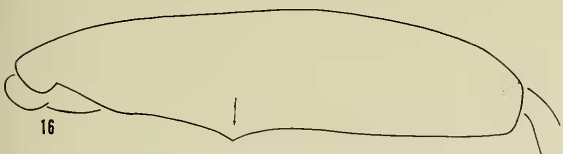

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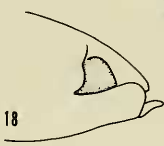

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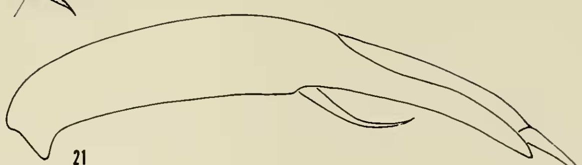

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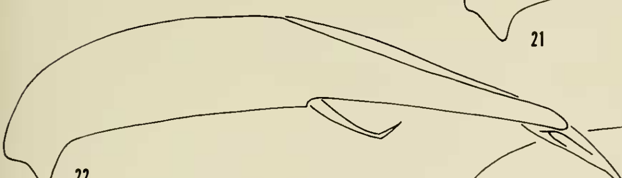

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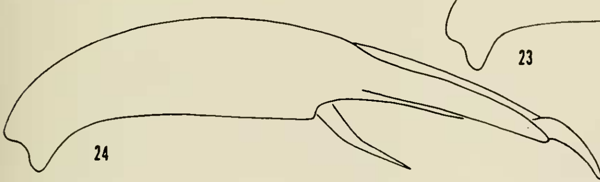

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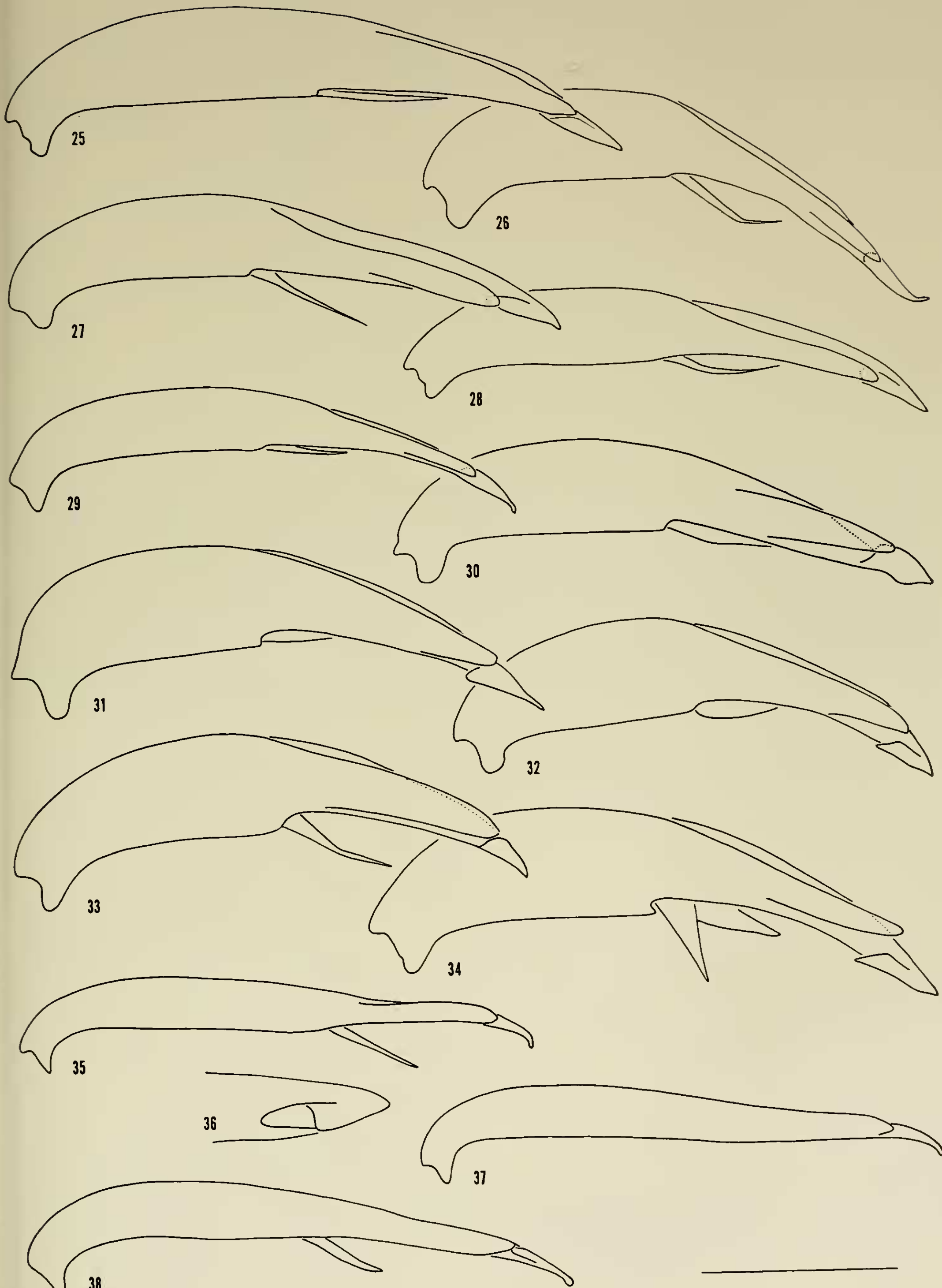
Figures 25–38, aedeagi of *Ptomaphagus*. Scale line in lower right 0.5 mm for aedeagi lateral views, 0.3 mm for dorsal view of tip. Fig. 25, *P. barri*, Henpeck Mill Cave, Tennessee. Fig. 26, *P. hazelae*, Tumbling Rock Cave, Alabama. Fig. 27, *P. fiskei*, Mt. Cove Farm Cave, Georgia. Fig. 28, *P. walteri*, Bryant Cave, Alabama. Fig. 29, *P. whiteselli*, Sittons Cave, Georgia. Fig. 30, *P. valentinei*, Sauta Cave, Alabama. Fig. 31, *P. hatchi hatchi*, Rousseau Cave, Alabama. Fig. 32, *P. hatchi hatchi*, Dry Cave, Tennessee. Fig. 33, *P. hatchi fecundus*, Caney Hollow Cave, Tennessee. Fig. 34, *P. episcopus*, McHardin Cave, Alabama. Fig. 35, *P. hirtus*, Mammoth Cave, Kentucky. Fig. 36, same as 35. Fig. 37, *P. nicholasi*, Fogelpole Cave, Illinois. Fig. 38, *P. hubrichti*, Cripps Mill Cave, Tennessee.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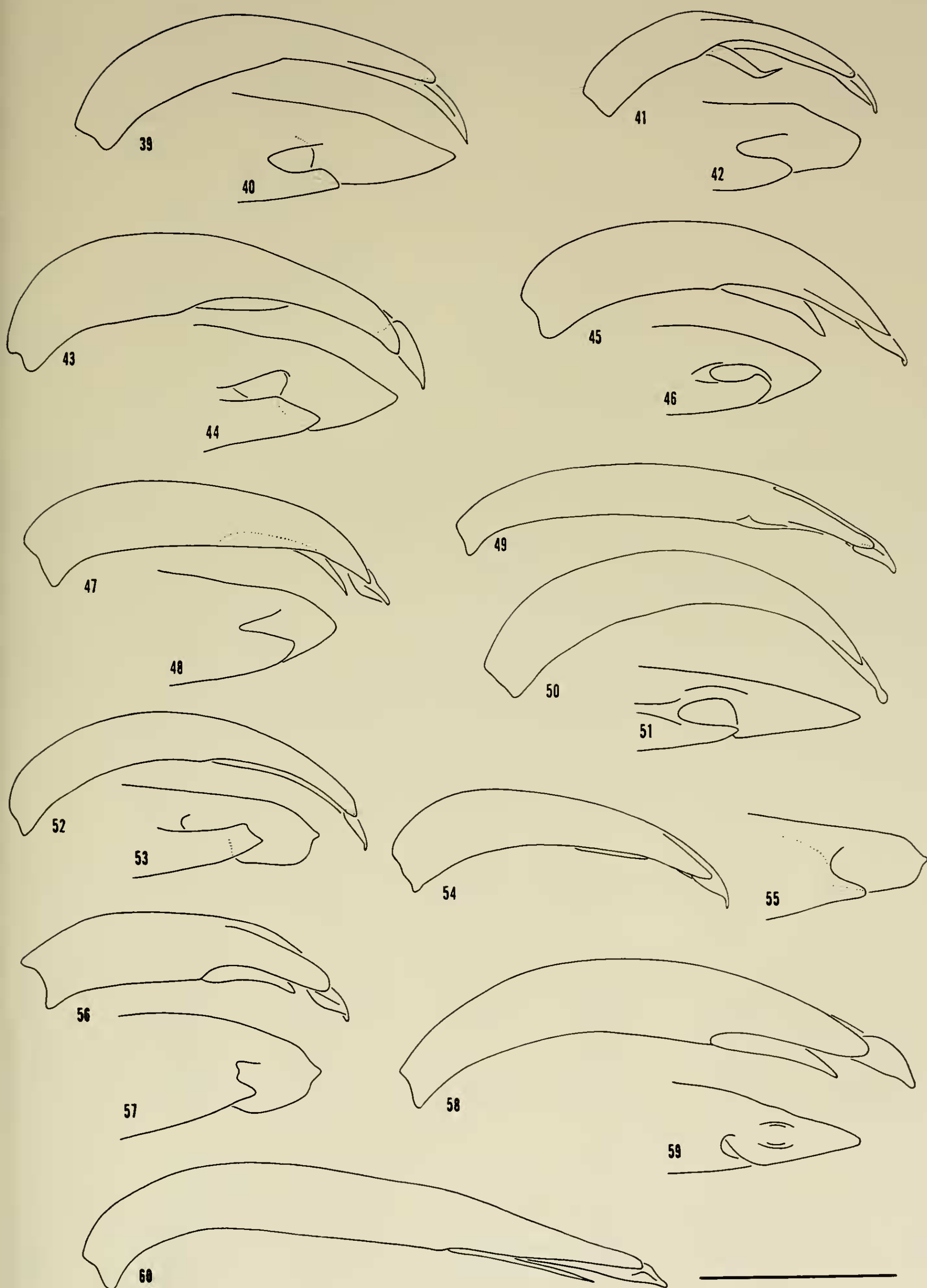
Figures 39–60, aedeagi of *Ptomaphagus*. Scale line in lower right 0.5 mm for aedeagi lateral views, 0.3 mm for aedeagal tips. Fig. 39, *P. cocytus*, Roaring Spring Cave, Arizona. Fig. 40, same as 39, dorsal view aedeagal tip. Fig. 41, *P. fisus*, Arizona, paratype 2996–5. Fig. 42, same as 41, dorsal view aedeagus tip. Fig. 43, *P. schwarzi*, holotype, Crescent City, Florida. Fig. 44, same as 43, dorsal view aedeagus tip. Fig. 45, *P. texanus*, Alachua Co., Florida. Fig. 46, same as 45, dorsal view aedeagus tip. Fig. 47, *P. californicus*, Danville, California. Fig. 48, same as 47, dorsal view aedeagus tip. Fig. 49, *P. giaquintoi*, Seamay Cave, Guatemala. Fig. 50, *P. nevadicus*, Danville, California. Fig. 51, same as 50, dorsal view aedeagus tip. Fig. 52, *P. consobrinus*, Alexandria, Louisiana. Fig. 53, same as 52, dorsal view aedeagus tip. Fig. 54, *P. brevior*, holotype, Putnam Co., Indiana. Fig. 55, same as 54, dorsal view aedeagus tip. Fig. 56, *P. ulkei*, Plummers Island, Maryland. Fig. 57, same as 56, dorsal view aedeagus tip. Fig. 58, *P. cavernicola*, Marvel Cave, Missouri. Fig. 59, same as 58, dorsal view aedeagus tip. Fig. 60, *P. troglomexicanus*, Cueva Capilla de la Perra, Mexico.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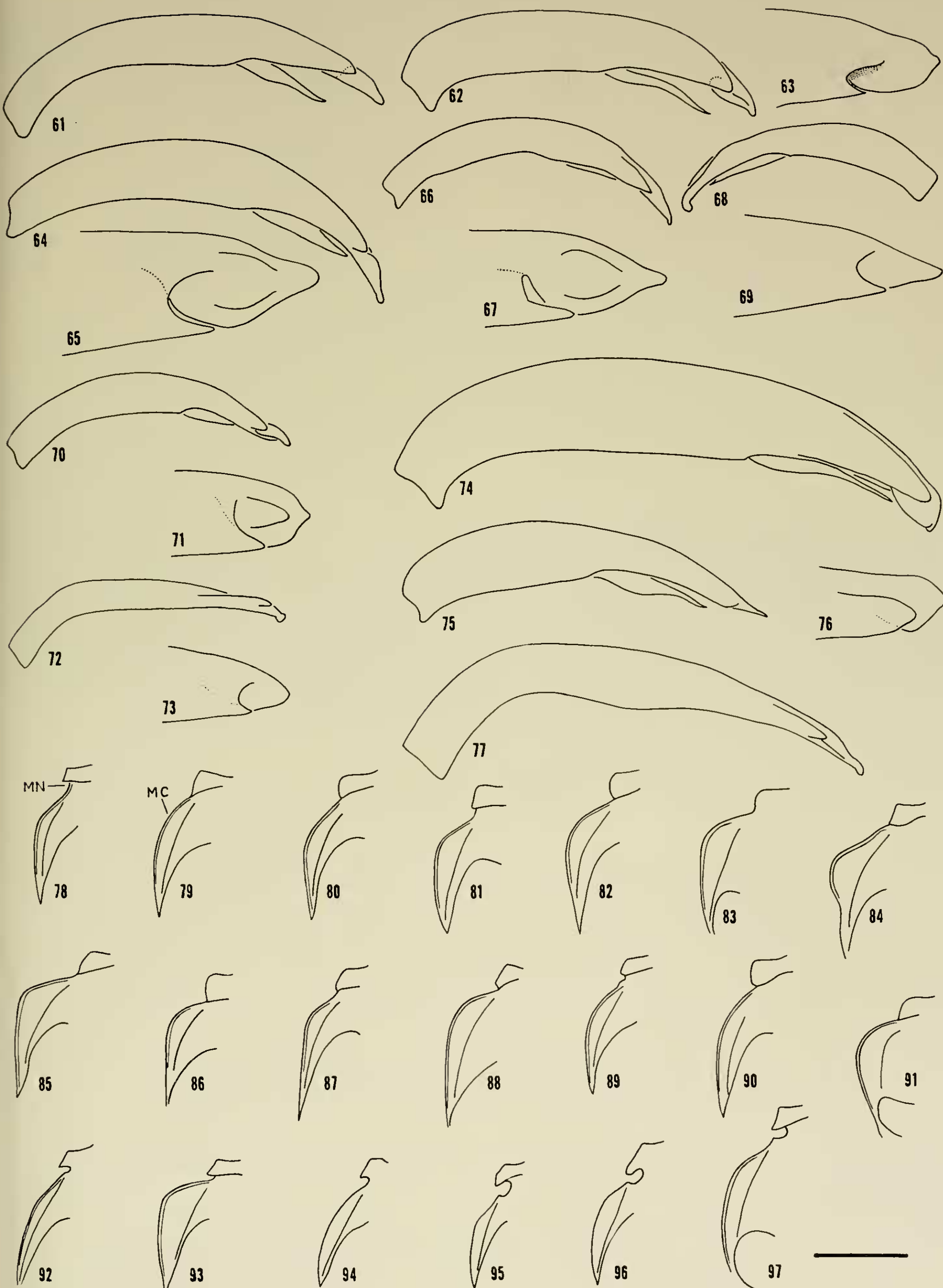
Figures 61–97. Figs. 61–77, aedeagi, lateral views, and dorsal views of aedeagal tips. Figs. 78–97, lateral view of left side of mesosternum. Fig. 61, *P. leo*, Chipinque Mesa, Mexico. Fig. 62, *P. elabra*, Cueva Pachón, Mexico. Fig. 63, same as 62. Fig. 64, *P. oaxaca*, Valle Nacional, Mexico. Fig. 65, same as 64. Fig. 66, *P. newtoni*, Valle Nacional, Mexico. Fig. 67, same as 66. Fig. 68, *P. altus*, San Cristóbal, Mexico. Fig. 69, same as 68. Fig. 70, *P. jamesi*, San Cristóbal, Mexico. Fig. 71, same as 70. Fig. 72, *P. spelaeus*, Gruta de Acuitlapan, Mexico. Fig. 73, same as 72. Fig. 74, *P. talamanca*, Volcán Chiriquí, Panama. Fig. 75, *P. meximontanus*, Tejamanil, Mexico. Fig. 76, same as 75. Fig. 77, *P. flabellatus*, São Paulo, Brasil. Fig. 78, *P. shapardi*, Devils Den, Arkansas. Fig. 79, *P. l. loedingi*, Shelta Cave, Alabama. Fig. 80, *P. loedingi longicornis*, Crossing Cave, Alabama. Fig. 81, *P. loedingi julius*, House of Happiness Cave, Alabama. Fig. 82, *P. loedingi solanum*, Sheldons Cave, Alabama. Fig. 83, *P. barri*, Henpeck Mill Cave, Tennessee. Fig. 84, *P. fiskei*, Mt. Cove Farm Cave, Georgia. Fig. 85, *P. walteri*, Bryant Cave, Alabama. Fig. 86, *P. whiteselli*, Sittons Cave, Georgia. Fig. 87, *P. valentinei*, Sauta Cave, Alabama. Fig. 88, *P. hatchi hatchi*, Crystal Cave, Tennessee. Fig. 89, *P. hatchi fecundus*, Caney Hollow Cave, Tennessee. Fig. 90, *P. episcopus*, McHardin Cave, Alabama. Fig. 91, *P. hirtus*, Mammoth Cave, Kentucky. Fig. 92, *P. texanus*, Austin, Texas. Fig. 93, *P. giaquintoi*, Cueva Seamay, Guatemala. Fig. 94, *P. consobrinus*, Alexandria, Louisiana. Fig. 95, *P. brevior*, Jefferson Co., Missouri. Fig. 96, *P. ulkei*, Madison Co., Kentucky. Fig. 97, *P. cavernicola*, Marvel Cave, Missouri. Aedeagi drawn to previous scale, scale line at bottom 0.5 mm for mesosterna. Abbreviations: mn, mesosternal notch; mc, mesosternal carina.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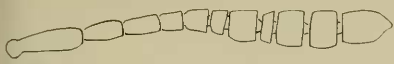
Figures 98–113, antennae. Scale line 1.0 mm. Fig. 98, *Adelopsis mitchellensis*, Mt. Mitchell, North Carolina. Fig. 99, *Ptomaphagus shapardi*. Devils Den State Park, Arkansas. Fig. 100, *P. loedingi loedingi*, Shelta Cave, Alabama. Fig. 101, *P. loedingi longicornis*, Crossing Cave, Alabama. Fig. 102, *P. loedingi julius*, House of Happiness Cave, Alabama. Fig. 103, *P. loedingi solanum*, Sheldons Cave, Alabama. Fig. 104, *P. barri*, Henpeck Mill Cave, Tennessee. Fig. 105, *P. hazelae*, Tumbling Rock Cave, Alabama. Fig. 106, *P. fiskei*, Mt. Cove Farm Cave, Georgia. Fig. 107, *P. walteri*, Bryant Cave, Alabama. Fig. 108, *P. whiteselli*, Sittons Cave, Georgia. Fig. 109, *P. valentinei*, Schiffman Cove Cave, Alabama. Fig. 110, *P. hatchi hatchi*, Dry Cave, Tennessee. Fig. 111, *P. hatchi hatchi*, Aladdin Cave, Alabama. Fig. 112, *P. hatchi fecundus*, Caney Hollow Cave, Tennessee. Fig. 113, *P. episcopus*, McHardin Cave, Alabama.



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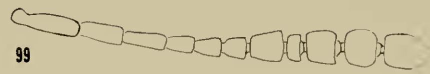

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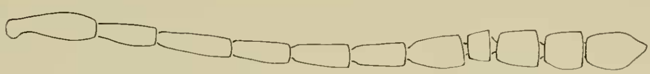

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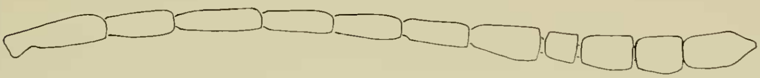

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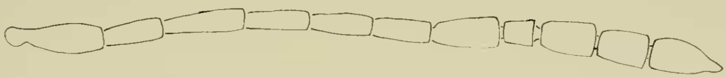

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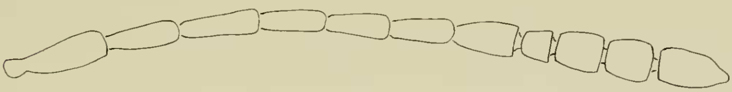

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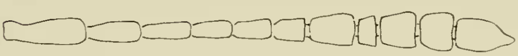

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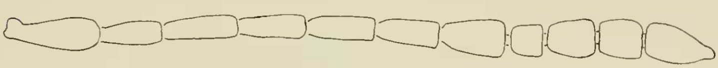

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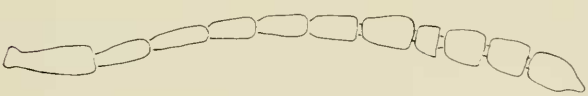

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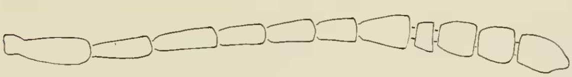

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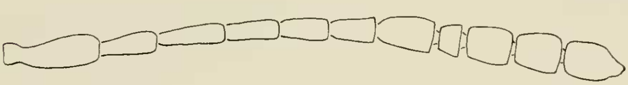
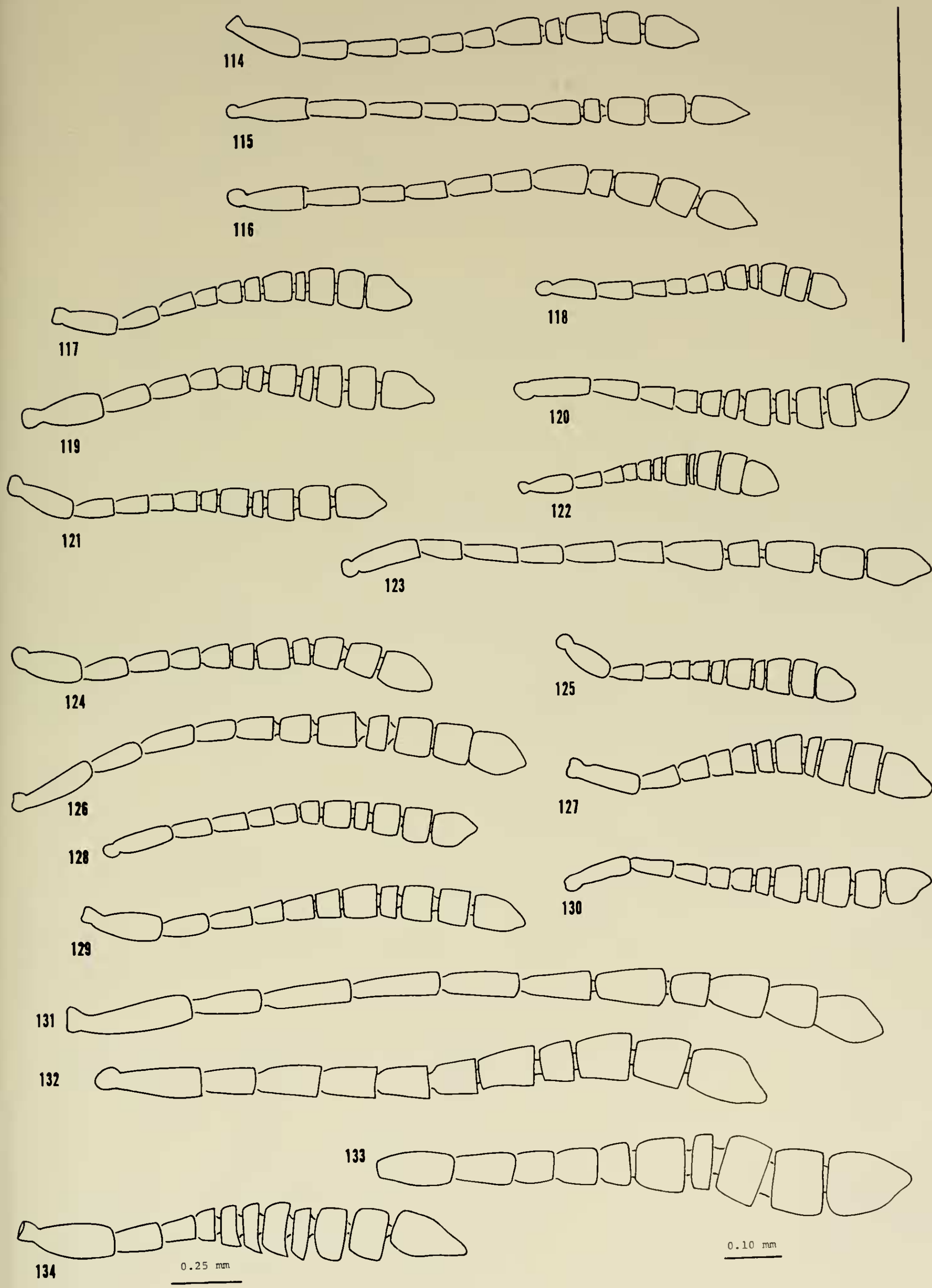


Figures 114–134, *Ptomaphagus* antennae. Scale line 1.0 mm for Figs. 114–132. Fig. 114, *P. hirtus*, Mammoth Cave, Kentucky. Fig. 115, *P. nicholasi*, Fogelpole Cave, Illinois. Fig. 116, *P. hubrichti*, Cripps Mill Cave, Tennessee. Fig. 117, *P. cocytus*, Roaring Springs Cave, Arizona. Fig. 118, *P. fisus*, Palm Springs, California. Fig. 119, *P. schwarzi*, Alachua Co., Florida. Fig. 120, *P. texanus*, Alachua Co., Florida. Fig. 121, *P. californicus*, Danville, California. Fig. 122, *P. brevior*, Jefferson Co., Missouri. Fig. 123, *P. giaquintoi*, Cueva Seamay, Guatemala. Fig. 124, *P. nevadicus*, Danville, California. Fig. 125, *P. consobrinus*, Alexandria, Louisiana. Fig. 126, *P. cavernicola*, Benton Co., Missouri. Fig. 127, *P. ulkei*, Madison Co., Kentucky. Fig. 128, *P. elabra*, Cueva El Pachón, Mexico. Fig. 129, *P. altus*, San Cristóbal, Mexico. Fig. 130, *P. leo*, Chipinque Mesa, Mexico. Fig. 131, *P. troglomexicanus*, Cueva Capilla, Mexico. Fig. 132, *P. talamanca*, Chiriquí, Panama. Fig. 133, *P. championi*, Santa Cruz del Quiché, Guatemala. Fig. 134, *P. flabellatus*, São Paulo, Brasil.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Figures 135–157. Figs. 135–138, female elytral apices. Figs. 139–157, dorsal views of spermathecae. Fig. 135, *P. oaxaca.* Fig. 136, *P. newtoni.* Fig. 137, *P. altus.* Fig. 138, *P. spelaeus.* Fig. 139, *Adelopsis mitchellensis*, Mt. Mitchell, N. Carolina. Fig. 140, *P. flabellatus*, São Paulo, Brasil. Fig. 141, *P. shapardi*, Devils Den State Park, Arkansas. Fig. 142, *P. loedingi loedingi*, Shelta Cave, Alabama. Fig. 143, *P. l. loedingi*, Pitts Cave, Alabama. Fig. 144, *P. loedingi longicornis*, Crossing Cave, Alabama. Fig. 145, *P. loedingi julius*, House of Happiness Cave, Alabama. Fig. 146, *P. loedingi solanum*, Sheldons Cave, Alabama. Fig. 147, *P. barri*, Henpeck Mill Cave, Tennessee. Fig. 148, *P. hazelae*, Tumbling Rock Cave, Alabama. Fig. 149, *P. fiskei*, Mt. Cave Farm Cave, Georgia. Fig. 150, *P. walteri*, Bryant Cave, Alabama. Fig. 151, *P. whiteselli*, Sittons Cave, Georgia. Fig. 152, *P. valentinei*, Schiffmans Cove Cave, Alabama. Fig. 153, *P. hatchi hatchi*, form I, Crystal Cave, Tennessee. Fig. 154, *P. h. hatchi*, form II, Doug Green Cave, Alabama. Fig. 155, *P. h. hatchi*, form III, Scott Cave, Alabama. Fig. 156, *P. hatchi fecundus*, Caney Hollow Cave, Tennessee. Fig. 157, *P. episcopus*, McHardin Cave, Alabama. Scale line 0.3 mm for spermathecae. Abbreviations of Fig. 139: R, right; L, left; P, posterior; A, anterior. All spermathecae drawn with this orientation.


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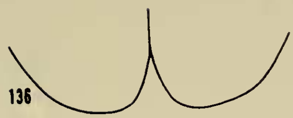
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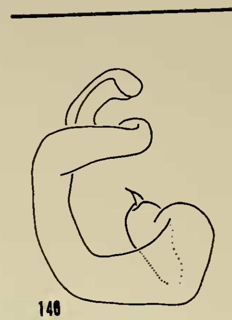
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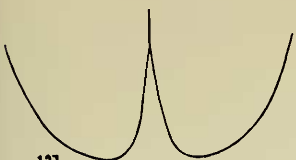
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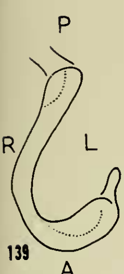

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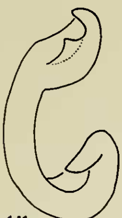
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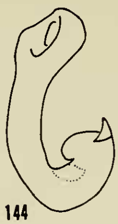
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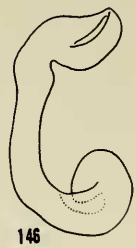
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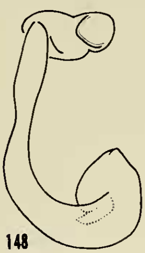
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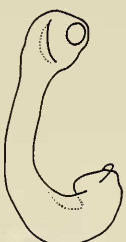
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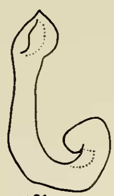
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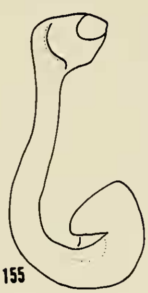
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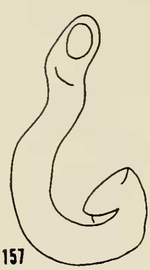
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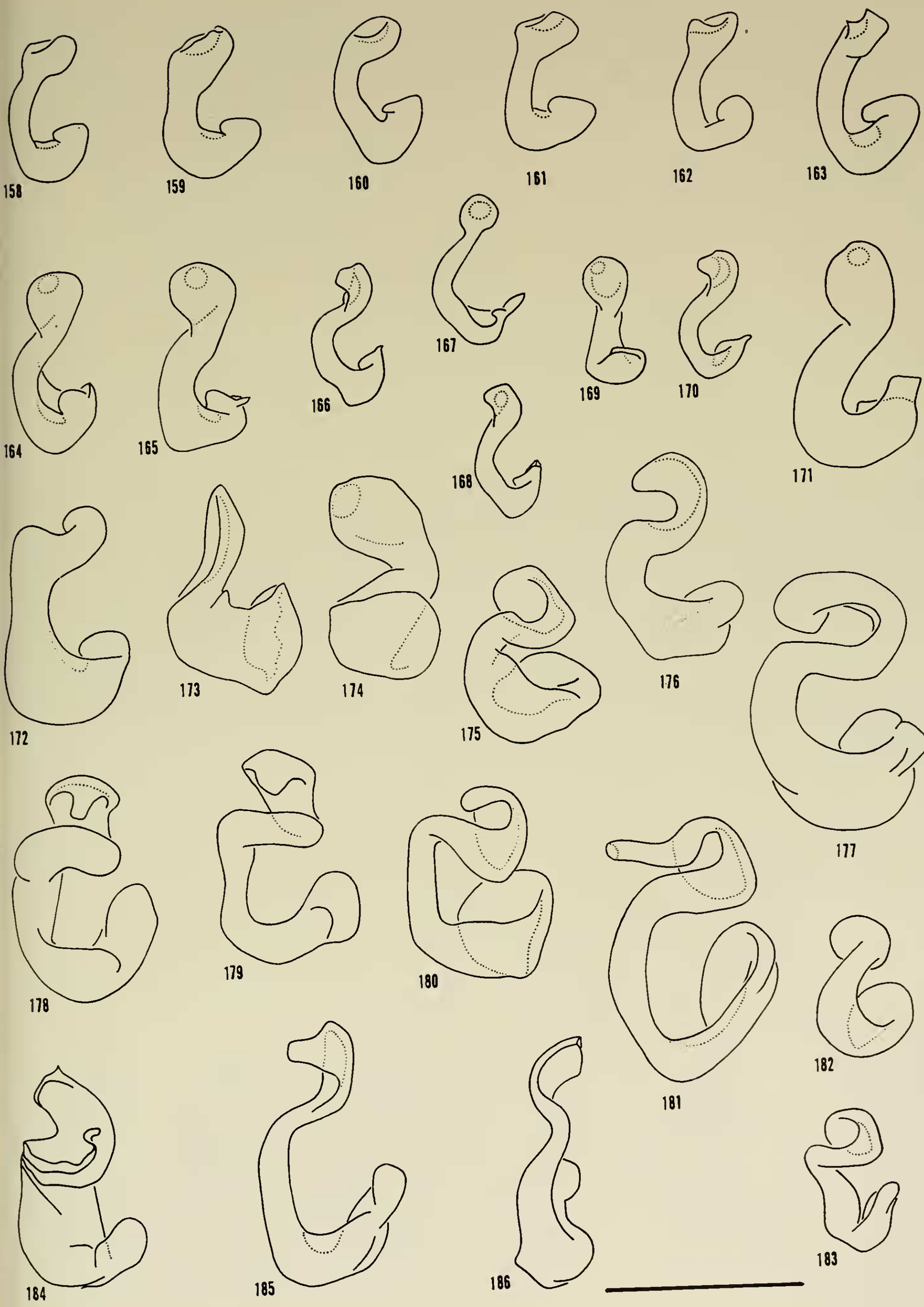
Figures 158–186, *Ptomaphagus* spermothecae. Fig. 158, *P. hirtus*, Mammoth Cave, Kentucky. Fig. 159, *P. hirtus*, Bypass Cave, Kentucky. Fig. 160, *P. hirtus*, Copelin Cave, Kentucky. Fig. 161, *P. hirtus*, Slick Rock Cave, Kentucky. Fig. 162, *P. nicholasi*, Fogelpole Cave, Illinois. Fig. 163, *P. hubrichti*, Cripps Mill Cave, Tennessee. Fig. 164, *P. cocytus*, Roaring Springs Cave, Arizona. Fig. 165, *P. fisus*, Pinal Mts., Arizona. Fig. 166, *P. fisus*, Palm Springs, California. Fig. 167, *P. fisus*, "S. Cal., 1879," (INHS). Fig. 168, *P. fisus*, paratype of *P. inermis*, Mexico. Fig. 169, *P. fisus*, Glenns Ferry, Idaho, view of left side. Fig. 170, same as 169, dorsal surface. Fig. 171, *P. schwarzi*, Alachua Co., Florida. Fig. 172, *P. texanus*, Alachua Co., Florida. Fig. 173, *P. californicus*, Danville, California. Fig. 174, same as 173, view of left side. Fig. 175, *P. giaquintoi*, Cueva Seamay, Guatemala. Fig. 176, *P. nevadicus*, Strawberry Res., Utah. Fig. 177, *P. nevadicus*, Danville, California. Fig. 178, *P. consobrinus*, lectotype, "Ga." Fig. 179, *P. consobrinus*, Lee Co., Texas. Fig. 180, *P. brevior*, Columbus, Texas. Fig. 181, *P. brevior*, Jefferson Co., Missouri. Fig. 182, *P. brevior*, San Antonio, Texas. Fig. 183, same as 182, view of right side. Fig. 184, *P. brevior*, teratology, Round Knob, N. Carolina. Fig. 185, *P. ulkei*, Limeton, Virginia. Fig. 186, *P. ulkei*, Madison Co., Kentucky, view of right side. Scale line at bottom 0.3 mm.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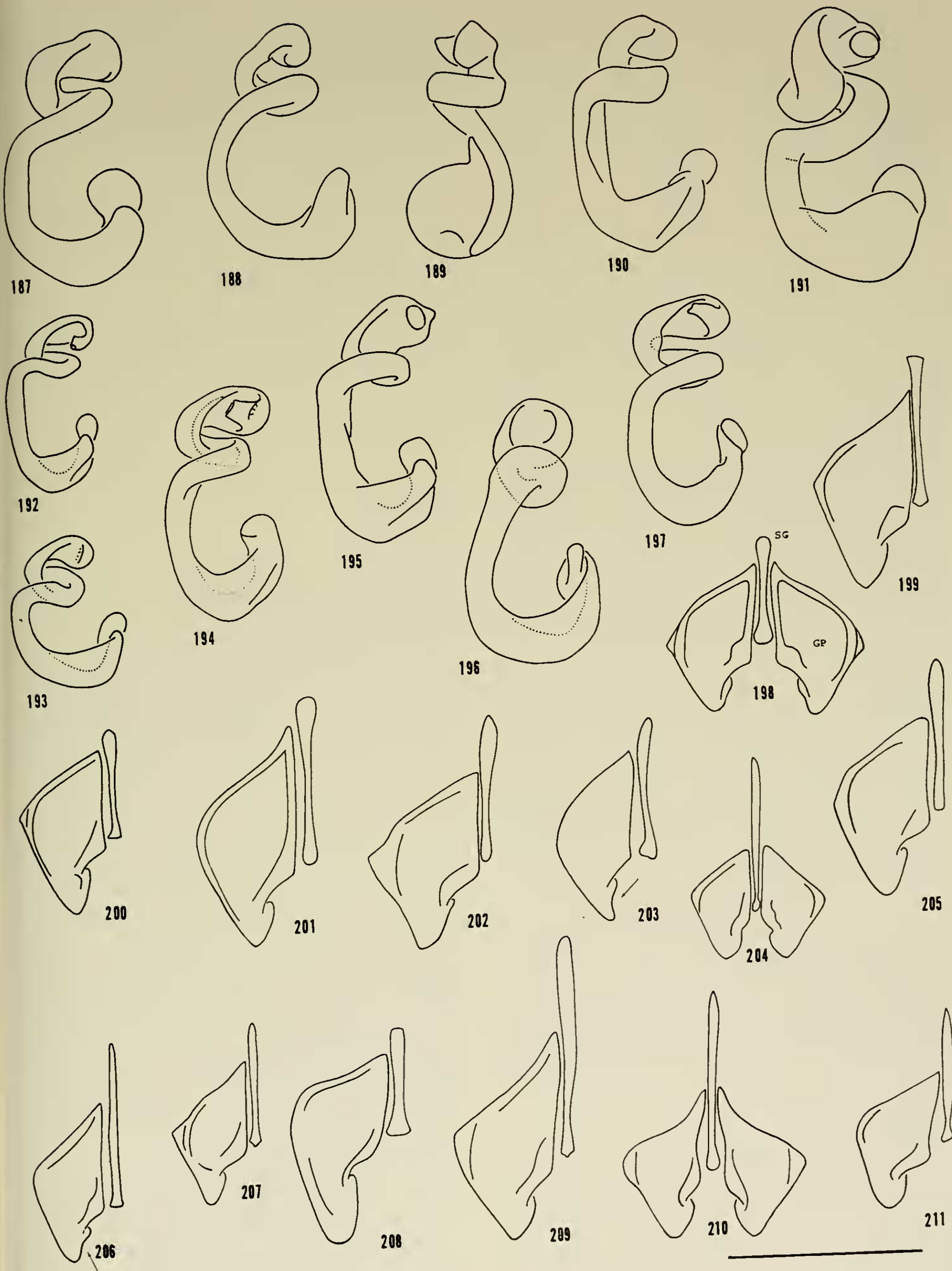
Figures 187–211. Figs. 187–197, *Ptomaphagus* spermathecae; Figs. 198–211, male genital segments. Scale line in lower right 0.3 mm for spermathecae, 0.5 mm for genital segments. Fig. 187, *P. cavernicola*, Benton Co., Arkansas. Fig. 188, *P. cavernicola*, Jackson Co., Florida. Fig. 189, same as 188, view of left side. Fig. 190, *P. troglomexicanus*, Cueva Copilla de la Perra, Mexico. Fig. 191, *P. oaxaca*, Valle Nacional, Mexico. Fig. 192, *P. spelaeus*, Gruta de Acuitlapan, Mexico. Fig. 193, *P. leo*, Chipinque Mesa, Mexico. Fig. 194, *P. altus*, San Cristóbal, Mexico. Fig. 195, *P. newtoni*, Valle Nacional, Mexico. Fig. 196, *P. elabra*, Cueva de El Pachón, Mexico. Fig. 197, *P. jamesi*, San Cristóbal, Mexico. Fig. 198, *Adelopsis mitchellensis*, Mt. Mitchell, North Carolina, s.g. = spiculum gastrale, g.p. = genital plate. Fig. 199, *P. cocytus*, Roaring Spring Cave, Arizona. Fig. 200, *P. fisus*, paratype 2996–5, Arizona. Fig. 201, *P. schwarzi*, holotype, Crescent City, Florida. Fig. 202, *P. texanus*, Alachua Co., Florida. Fig. 203, *P. californicus*, Danville, California. Fig. 204, *P. giaquintoi*, Cueva Seamay, Guatemala. Fig. 205, *P. nevadicus*, Danville, California. Fig. 206, *P. consobrinus*, Alexandria, Louisiana. Fig. 207, *P. brevior*, Middlesex Fells, Massachusetts. Fig. 208, *P. ulkei*, Plummers Island, Maryland. Fig. 209, *P. cavernicola*, Marvel Cave, Missouri. Fig. 210, *P. leo*, Chipinque Mesa, Mexico. Fig. 211, *P. elabra*, Cueva de El Pachón, Mexico.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Ptomaphagus cocytus new species
Figures 16, 39, 40, 117, 164, 199; Map 10

Holotype male and allotype female in MCZ (no. 31893). Type locality: Arizona, Coconino County, Kaibab Plateau, Roaring Springs Cave. Type data: 1.i.1965, Gregory Lane leg. Paratypes, 2 females, same locality, 16.iv.1965, L. Ball and G. T. Lane leg., in SBP.

Diagnosis. The tooth on the male metafemur distinguishes the species from all others except *fisus,* from which it is separated by the reduced wings, elongated appendages, and drawn-out female elytral apex.

Description. Length 3.2–3.4 mm. Width 1.4–1.5 mm. Color pale yellowish brown. Head finely punctured and pubescent. Eyes pigmented, faceted, reduced; horizontal diameter 1.4 times the distance between their anterior margin and antennal socket. Antennae (Fig. 117) not reaching pronotal base when laid back; segments II and III longer than broad; IV and V subquadrate; VI–X wider than long. Pronotum widest at middle, only slightly narrower at base; 1.55 times wider at base than long. Elytra 1.55 times as long as wide at base; slightly wider 1/4 behind base; external apical angles effaced; female apex obliquely truncate, drawn out; male apex obliquely truncate and rounded. Wings reduced to 3/4 the length of elytra. Mesosternal notch present but reduced. Legs elongated, male metafemur with tooth (Fig. 16). Aedeagus (Fig. 39) regularly curved, thin; tip in dorsal view (Fig. 40) sharp. Genital plates anteriorly elongated to enclose most of spiculum (Fig. 199). Spermatheca (Fig. 164) small, central shaft curved, posterior end slightly swollen, anterior end with small crest.

Variation. No variation noted.

Etymology. Cocytus, a noun used in apposition, is the name of the River of Wailing, one of the five rivers of Hades, referring to the type locality, Roaring Springs Cave.

Field notes. I visited the type locality in September 1969, but was unable to collect carefully, and found no beetles. Roaring Springs Cave lies behind Roaring Springs, which is currently being prepared as a water source for the south rim of Grand Canyon National Park. This may restrict future collecting in the cave.

The cave, with its several entrances, and about two miles of mapped passage, lies in the Cambrian Muav Limestone on top of the Bright Angel Shale. It is at an approximate elevation of 5200 feet, or 3000 feet below, and 4.2 miles from, the head of the Kaibab Trail, which is used to reach it from North Rim of Grand Canyon National Park.

Seasonality. If the species is cave-adapted, it should not be expected to show a reproductive seasonality. Larvae are unknown.

Distribution. The species is now known only from the type series of four specimens from Roaring Springs Cave.

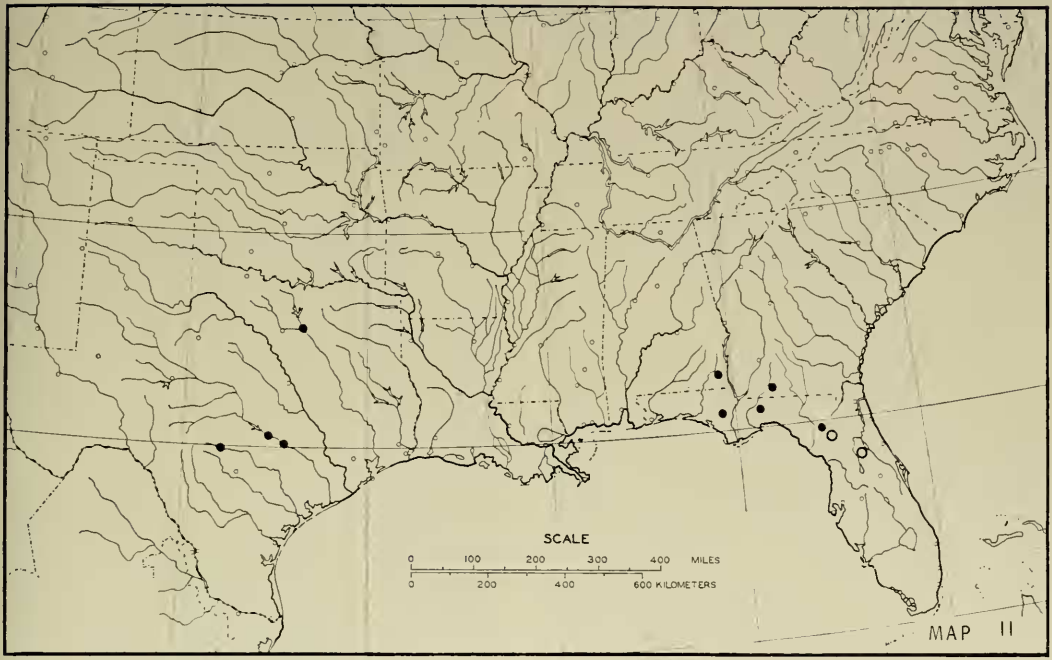
Distributional comments. Several other caves are known in the north rim of Grand Canyon. Roaring Springs Cave is the largest and most accessible. From what little I know of the other smaller and drier caves, it seems less likely that they would be additional localities for this species.

The species may be limited to the type locality. The reduced wings and long legs suggest that it is cave-adapted, and incapable of dispersing in the xeric epigean environment in the bottom of the canyon. It also seems unlikely that there is much chance for extensive underground dispersal. The great depth of the limestone beneath the Kaibab Plateau and its comparative thinness have probably not led to development of extensive and interconnecting systems of air-filled cave passageways.

Ptomaphagus schwarzi Hatch
Figures 43, 44, 119, 171, 201; Map 11

Ptomaphagus schwarzi Hatch, 1933: 203. Holotype male in USNM (no. 43481), seen. Type locality: Florida, Crescent City.

Ptomaphagus (*Adelops*) *schwarzi,* Jeannel, 1936: 91; 1949: 97.



Map 11. Distribution of *Ptomaphagus* (*Adelops*) *schwarzi* (open circles) and *Ptomaphagus* (*Adelops*) *texanus* (dark dots).

Diagnosis. The species is distinguished by its fine striae, light brown color, reduced eyes, and the shape of the spermatheca.

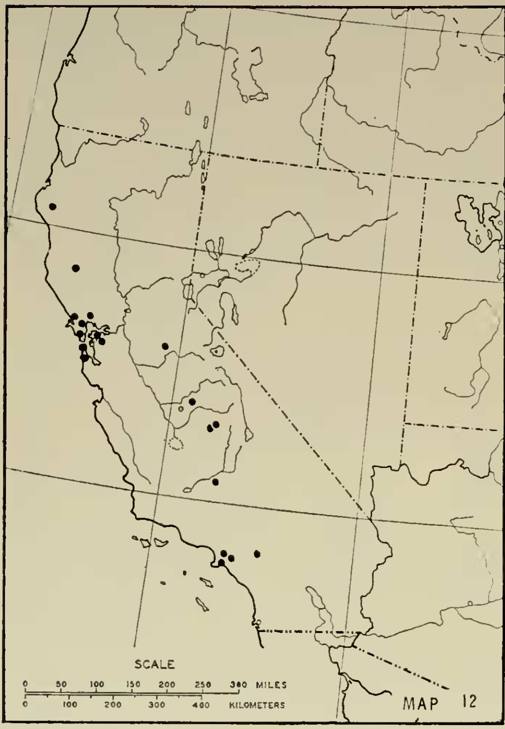
Description. Length 2.7–3.6 mm. Width 1.2–1.7 mm. Color pale yellowish brown. Head finely, densely pubescent. Eyes reduced, pigmented, faceted; their horizontal diameter 1.15 times the width between anterior margin and edge of antennal socket. Antennae (Fig. 119) short, not reaching base of pronotum when laid back; segments II–V longer than broad, VI–X broader than long. Pronotum widest, but only slightly, 1/3 before base; 1.4 times wider at base than long; sides parallel behind, converging in front; hind angles right; hind margin sinuous. Elytra widest 1/4 behind base; 1.5 times longer than wide at base; external apical angles effaced; female sutural angle sharp, apex oblique, sinuous, drawn out; male apex oblique, not drawn out at sutural angle. Mesosternal notch present. Legs with protibial spurs unusually well developed. Aedeagus (Fig. 43) widest near base, curved, gradually narrowing toward tip; in dorsal view tip (Fig. 44) pointed. Spiculum gastrale short and enclosed by slightly anteriorly elongated genital plates (Fig. 201). Spermatheca (Fig. 171) stout; shaft slightly curved, anterior end with low crest, posterior end with curve and bulge.

Variation. No variation noted.

Field notes. The species may be restricted to pocket gopher (*Geomys*) burrows in Florida. Data is not available for the habitat of the holotype, but four of the five other known specimens were taken in *Geomys* burrows.

Seasonality. Only adults are known from January, May, and September collections. The specimen collected in a malt trap in January may indicate the time of dispersal by flight.

Distribution. The species is apparently restricted to pocket gopher burrows in central peninsular Florida. I have seen



Map 12. Distribution of *Ptomaphagus (Adelops) californicus.*

six specimens from the following four localities: FLORIDA. *Alachua County:* Devils Millhopper (*Geomys* burrow), 2 (FSCA); no locality (B. A. Barrington, *Geomys* burrow no. 11, 13.IX.1939), 2 (UMMZ). *Putnam County:* Crescent City, 1 (USNM).

Distributional comments. The species may belong to the suite of arthropods that diverged and speciated when peninsular Florida was isolated as an island during the higher sea levels of the major interglacials (reviewed *in* Howden, 1969: 47). An extensive report on the fauna of the Florida pocket gopher burrows is that of Hubbell and Goff (1940). The several specimens of *Ptomaphagus* that they report from pocket gopher burrows at Newnans Lake, Alachua County, are probably this species but the location of the specimens is not known.

Since the adults are winged, distribution and dispersal is not necessarily limited to and by pocket gopher burrow systems.

Ptomaphagus texanus Melander
Figures 45, 46, 92, 120, 172, 202; Map 11

Ptomaphagus texanus Melander, 1902: 329. Lectotype here designated as USNM specimen bearing red label "cotype no. 6618," from syntype series; lectotype also bears label "Austin Tx 11.19.1.," seen. Five paralectotypes seen from same locality, 3 collected 11.19.1901, 2 11.16. 1901. Type locality: Texas, Austin. Hatch, 1933: 204.

Ptomaphagus (Adelops) texanus, Jeannel, 1936: 92.

Diagnosis. The species is partially characterized by its range in the Gulf Coastal States, habits of living in ant nests and vertebrate burrows, large eyes, generally light-colored elytra and darker pronotum, and oblique female elytral apex. It is clearly distinguished by the shape of the spermatheca, and male genital structures.

Description. Length 2.6–3.2 mm. Width 1.0–1.5 mm. Color light to dark brown, generally with elytra lighter than head and pronotum. Head finely punctured and pubescent. Eyes large, their horizontal diameter 3.3 times as wide as the space between their anterior margin and antennal socket. Antennae (Fig. 120) short, reaching to base of pronotum when laid back; segments II–III longer than broad, IV–X broader than long. Pronotum widest at base; 1.6 times wider than long; sides parallel behind. Elytra widest 1/4 behind base; 1.6 times longer than wide; external apical angles effaced; male apex rounded; female apex obliquely truncate. Mesosternal notch present (Fig. 92). Aedeagus (Fig. 45) gently curved, narrowing gradually to tip; tip in dorsal view moderately pointed (Fig. 46). Spiculum gastrale long, 1/2 enclosed by genital plates (Fig. 202). Spermatheca (Fig. 172) with stout, fairly straight central shaft, anterior end broadly hooked, posterior end bilobed with dent.

Variation. Differences have been noticed

in the genital segments between Florida and Texas populations. The spiculum is slenderer and the genital plates broader in Texas material. The spermatheca shows only minor differences, being slightly thinner with a slightly broader anterior end in Texas material.

Field notes. Melander (1902) reported taking 10 males and 13 females in simple pitfall traps at the entrances to nests of *Pogonomyrmex barbatus,* harvester ants, at Austin, Texas, in November. Four were taken by H. Howden in malt traps at Kerrville, Texas. Alabama and Georgia specimens were taken in old field mouse nests. All Florida material was taken in gopher tortoise (*Gopherus*) burrows, or in malt-proprionic acid traps in the burrows. I tried Melander's methods in June in central Texas and captured only several thousand *Pogonomyrmex* and several painful stings. Perhaps at this time of year the ants are more active and the beetles less active than those Melander encountered in November.

Seasonality. Vertebrate nest and burrow collections have been made in February, March, and April. Ant nest collections are from November. Malt trap collections are from April. The species may exist as adults in nest-burrow habitats throughout the year. They apparently are active in the winter months, leaving ant nests to disperse or forage, and were probably dispersing by flight when taken in malt traps in April. Larvae are unknown.

Distribution. The species is known only from southern Gulf Coastal Plain localities. I have seen 50 specimens from the following 11 localities:

ALABAMA. *Dale County:* Mobile, Typhus Lab (old field mouse nest), 2 (USNM). FLORIDA. *Alachua County:* "Sta. 6, *Gopherus* burrow," 16 (FSCA); High Springs (4 mi. N, *Gopherus* burrow), 11 (HAHC). *Calhoun County:* Clarksville (tortoise burrow), 3 (HAHC). *Gilchrist County:* Trenton (*Gopherus* burrow no. 5, 14 ft. from entrance), 3 (FSCA). *Leon County:* Tallahassee, 1 (HAHC). GEORGIA. *Thomas County:* Thomasville (old field mouse nest), 2 (USNM). TEXAS. *Bastrop County:* Bastrop St. Pk., 1 (CNCI). *Dallas County:* Dallas, 1 (INHS). *Kerr County:* Kerrville (malt trap), 4 (CNCI). *Travis County:* Austin, 6 (USNM, MCZ, AMNH, FMNH).

Distributional comments. The species probably actively disperses in cooler months. As presently known it generally inhabits ant nests in Texas and not in Florida, and inhabits vertebrate nests and burrows in Florida and not in Texas. I believe this is a reflection of inattention given to these hard-to-collect habitats in both regions. If the beetle can inhabit the nests of *Pogonomyrmex barbatus* throughout the range of this ant, a very large distributional range is possible. Cole (1968: 57) shows the ant to occur throughout most of Mexico, all of Texas and Oklahoma, and westward to Arizona, and north to eastern Colorado. East of the Mississippi River another ant species, *P. badius,* is widely distributed and may be an alternate but as yet unexamined host for the beetle.

Ptomaphagus were reported by Hubbard (1894, 1896) and Young and Goff (1939) as *Gopherus* burrow inhabitants at DeFuniak Springs, and Crescent City, Florida. The specimens they treat as *ulkei* from DeFuniak Springs probably were *texanus.* Two specimens from tortoise burrows at Crescent City were *consobrinus.*

Ptomaphagus californicus (Leconte)

Figures 47, 48, 121, 173, 174, 203; Map 12

Catops californicus Leconte, 1854: 281. Lectotype here designated as female in MCZ (Leconte coll.) bearing red label with "type 3153–3" and a gold disc, seen. Murray, 1856: 458.

Ptomaphagus californicus, Horn, 1880: 263; Hatch, 1957: 42.

not *Ptomaphagus californicus,* Hatch, 1933: 203.

not *Ptomaphagus* (*Adelops*) *californicus,* Jeannel, 1936: 91; 1949: 97.

Ptomaphagus latior Hatch, 1933: 204. Holotype

male in CAS (no. 2301), seen. Synonymy implied by Hatch, 1957: 42, and I agree with this.

Diagnosis. The species is known only from California. It can be separated from all others by the shape of the spermatheca. This is the only species besides *consobrinus* having a curve on the edge of the genital plate bordering the genital orifice.

Description. Length 2.4–3.0 mm. Width 1.3–1.5 mm. Color medium to dark brown, head and elytra usually darker than elytra. Head finely striate. Eyes somewhat reduced; their horizontal diameter 1.4 times wider than space between their anterior edge and antennal socket edge. Antennae (Fig. 121) somewhat elongate, reaching base of pronotum when laid back; segments II–V and VIII longer than wide, VI and VIII–X wider than long. Pronotum widest at base 1.6 times as wide as long; sides sub-parallel behind; hind angles right, hind margin straight. Elytra 1.4 times as long as wide at base; female apex obliquely truncate, male apex rounded-truncate. Mesosternal notch as in *consobrinus* (Fig. 94). Aedeagus (Fig. 47) fairly straight, curved down at tip; dorsal view of tip (Fig. 48) bluntly rounded. Genital plates not elongated anteriorly along thin spiculum, which is more than 3/4 enclosed; concavity in edge of plate bordering genital orifice (arrow, Fig. 203). Spermatheca (Figs. 173, 174) very flattened in center and at both ends; twisted.

Variation. No variation noted.

Field notes. The information that is available suggests that the species is a general scavenger in the more mesic areas of California. Many specimens were taken in the debris and nests of ground-dwelling *Vespula* (*pennsylvanica*?, F. X. Williams det.) wasps. Many have been taken at Danville, California: 1 in a shrew nest, 1 at the entrance of a fresh pocket gopher burrow, 3 in a pocket gopher nest, and 1 in a field mouse nest under sheet metal. Two are from a small dirt cave in Napa County, California. Two from Alameda County are from under yellow cup fungi. One was taken from the hair of a *Neotoma* rat (alive?) and a series of 11 described as *P. latior* came from a *Neotoma* nest.

Seasonality. Collections of the species are known from every month except September. There may be no reproductive seasonality in protected sites such as *Neotoma* nests and pocket gopher burrows. Free-living forest inhabitants are probably influenced by the dry California summers, and are more active in the wet winter months. Larvae are not known.

Distribution. The species is known to me only from California, and is probably most abundant in mesic forest habitats. I have seen 60 specimens from the following localities:

CALIFORNIA. *Alameda County:* Oakland (hills back of, under yellow cup fungus), 2 (CAS); No locality, 1 (MCZ). *Contra Costa County:* Danville, 1 in shrew nest, 1 in entrance of fresh gopher burrow, 3 in gopher nests, 1 in field mouse nest, 17 in debris *Vespula* nests, (CAS). *Humboldt County:* Redwood Creek (Blairs Ranch), 1 (USNM). *Kern County:* no locality, 1 (MCZ). *Lake County:* Hullville, 1 (FMNH). *Los Angeles County:* Coquilett, 1 (USNM); Los Angeles, 1 (ANSP); Pasadena, 2 (CAS); Pomona, 2 (MCZ). *Madera County:* North Fork (*Neotoma* nest), 6 (CAS, CUIC) (all paratypes of *P. latior*). *Marin County:* Fairfax, 5 (CAS). *Napa County:* White Cave (4 mi. E St. Helena), 2 (CAS). *San Bernardino County:* San Bernardino Mts., 2 (MCZ). *San Francisco County:* San Francisco, 1 (CAS). *San Mateo County:* Edgemar, 1 (CAS). *Sonoma County:* Forestville (in marsh), 2 (CAS); Sobra Vista, 1 (CAS); "S. Sonoma Co." (*Neotoma* hair), 1 (CAS). *Tulare County:* Kaweah (1 at 1000′), 2 (CAS); Sequoia National Park (Potwisha), 1 (CAS). *Tuolumne County:* Twain-Harte (4000′), 1 (CAS).

Distributional comments. Hatch (1957: 42) records the species from southwestern Idaho. This is based upon the name in a

Map 13. Distribution of Mexican and Central American *Ptomaphagus*. None are known from the West Indian Islands.

list of beetles from Atlanta, Idaho, reported by Leconte in 1878. I believe that the record probably represents another species.

Ptomaphagus giaquintoi Jeannel
Figures 49, 93, 123, 175, 204; Map 13

Ptomaphagus (*Adelops*) *giaquintoi* Jeannel, 1936: 93. Type in MNHN, Paris, seen. Type locality: Guatemala, Sepacuite Cave, near Panzos, Alta Verapaz. Jeannel, 1949: 98.

Diagnosis. This is the only *Ptomaphagus* known from caves in Guatemala. It is the only species known from Guatemala and Mexico, other than *troglomexicanus* and *gypsum*, which shows cave adaptations, having long antennae reaching beyond the pronotum when laid back. The possession of wings and pigmented eyes whose horizontal width equals the space between the eye and the antennal base separates it from *troglomexicanus* and *gypsum*.

Description. Length 2.0–3.0 mm. Width 0.9–1.3 mm. Color light to dark brown. Head faintly punctured. Eyes reduced in size, faceted, pigmented; width of head from antennal base to margin across eyes 2.0–2.3 times width of eyes. Antennae (Fig. 123) elongate, narrow, reaching first third of elytra when laid back; segment III four times as long as wide, longer than II; segments IV, V, and VI subequal, three times as long as wide, longer than II; VII twice as oblong as wide, conical; VIII longer than wide; IX and X longer than

wide. Pronotum clearly transverse, at base 1.75 times as wide as long; widest at base, sides widening gradually to base; hind margin slightly sinuous. Elytra widest slightly behind base; 1.6 times as long as wide at base; external apical angles rounded; apex oblique in female, rounded in male. Wings present and large, not observed in flight; but I see no reason to doubt that they function in flight. Mesosternal carina (Fig. 93) high and prominent; notch conspicuous. Aedeagus (Fig. 49) long, slender, slightly curved; in dorsal view tip broadly pointed. Spiculum gastrale very long and thin; projecting more than twice its length beyond genital plates (Fig. 204). Spermatheca (Fig. 175) compact, broad, heavily twisted, expanded and flattened at anterior and posterior ends.

Variation. No variation noted. I do not find the pubescence to be as long and uneven as did Jeannel (1936: 81), nor do the antennae match his description.

Etymology. The species was named for the collector of the type series, Dr. Giaquinto Mira, an Italian physician who studied malaria and sleeping sickness in Guatemala in 1933 (personal communication with Dennis Koester, Finca Seamay).

Field notes. A series of 44 specimens was taken in 1948 on dead bats in Cueva de Lanquin, by R. D. Mitchell (FMNH). I took 41 in Cueva Seamay and 86 in Cueva de Lanquin on dryish guano of insectivorous bats and 36 on moist guano beneath a roost of insectivorous emballonurid bats (*Balantiopteryx plicata,* my determination) in Cueva Sepacuite. The beetles were not attracted to carrion-baited traps in Cueva Seamay, nor found at guano and waste of frugivorous bats. In each cave the beetles were found only in a single small localized area.

The cave air and soil temperatures were 67°F in Cueva Seamay; Lanquin Cave, 2100 feet lower in elevation, had an air and soil temperature of 74°F and 73°F respectively.

Seasonality. Collections have been made only in June and August. Teneral adults were taken only in Lanquin Cave (10 out of 86 in August and 6 out of 44 in June). Larvae are known only from my August collection in Lanquin Cave. Any seasonality in the species is probably related to the wet-dry season of this section of Guatemala.

Distribution. Known from three limestone caves in the Guatemalan Department of Alta Verapaz. The maximum linear extent of the known range is 20 km. I have seen 207 specimens from the following localities: **GUATEMALA.** *Dept. Alta Verapaz*: Cueva de Lanquin, 1000′ elev. (at Lanquin), 130 (FMNH, SBP); Cueva Seamay, 3100′ elev. (at Finca Seamay, Senahu), 41 (SBP); Cueva Sepacuite (No. 2), 3500′ (?) elev. (at Finca Sepacuite, Senahu), 36 (SBP).

Distributional comments. Doubt exists as to the identity of the type locality. It is reasonable that Cueva Sepacuite is on Finca Sepacuite, 6.1 road miles from the junction 0.9 miles before Senahu. Three caves exist at Finca Sepacuite, and all were explored and collected. Only one was large and contained beetles, and I believe it to be the cave in which Dr. Mira collected. I will treat these caves and their fauna in a later paper, in my series on the faunas of tropical American caves (Peck, 1971a).

The species can be expected to have a larger range than is now known. Its long antennae and reduced eyes suggest cave specialization, but the large wings do not suggest that the species is unable to disperse by flight. Numerous unexplored and uncollected limestone caves exist in the lowlands and highlands of northern Guatemala, and adjacent Mexico and Belice. Sufficient collecting has not been accomplished to know if the species is absent from lowland caves remote from montane regions.

Map 14. Partial distribution of *Ptomaphagus* (*Adelops*) *nevadicus*. Localities not shown are Whitford Lake, 70 mi. ENE of Edmonton, Alberta, Canada, and El Salta, 55 mi. WSW of Durango, Mexico.

Ptomaphagus nevadicus Horn
Figures 50, 51, 124, 176, 177, 205; Maps 13, 14

Ptomaphagus nevadicus Horn, 1880: 263. Lectotype here designated as female in ANSP (no. 2997), seen. Type locality: "western Nevada." Hatch, 1933: 203.

Ptomaphagus californicus Leconte, Hatch, 1933: 203.

Ptomaphagus (*Adelops*) *californicus californicus* Leconte, Jeannel, 1936: 91; 1949: 97.

Ptomaphagus (*Adelops*) *californicus nevadicus* Horn, Jeannel, 1936: 91.

Ptomaphagus piperi Hatch, 1933: 204. NEW SYNONYMY. Holotype female in USNM (no. 43482), seen. Type locality: Washington, Pullman. Hatch, 1957: 42.

Ptomaphagus (*Adelops*) *piperi*, Jeannel, 1936: 91; 1949: 97.

Ptomaphagus thomomysi Hatch, 1957: 42. NEW SYNONYMY. Holotype female in UBCZ, no number, Stace Smith collection, seen. Type locality: British Columbia, Creston.

Ptomaphagus densus Hatch, 1957: 42. NEW SYNONYMY. Holotype male in Burke Museum, University of Washington, Seattle, not seen. Type locality: Oregon, Forest Grove.

Diagnosis. The species is separated from all others by the long, thin, curved aedeagus, and the shape of the spermatheca.

Description. Length 2.5–3.3 mm. Width 1.3–1.5 mm. Color light to dark brown, head and pronotum darker than elytra, antennal base lighter. Head with faint striae. Eyes normal to slightly reduced, their horizontal diameter 1.3–1.9 times width of space between antennal socket

and anterior margin. Antennae (Fig. 124) normal, barely reaching base of pronotum when laid back; segments II–V and VII longer than wide, segments VI and VIII–X wider than long. Pronotum widest at base; 1.5–1.7 times as wide at base as long; sides nearly parallel behind; hind margin straight or slightly sinuous. Elytra 1.3–1.5 times as wide as long at base; apex rounded in males, obliquely truncate in females at suture, little to distinctly drawn out with little to distinct sinuation in margin; striae fine to coarse, transverse to oblique. Mesosternal notch low as in *consobrinus* (Fig. 94). Aedeagus (Fig. 50) long, thin, curved; tip with button; in dorsal view (Fig. 51) finely pointed. Spiculum gastrale long and thin, 2/3 to 1/2 enclosed by genital plates which are not anteriorly elongated (Fig. 205). Spermatheca (Fig. 176, 177) slightly flattened at posterior end, broadly flattened with low knob at anterior end.

Variation. This species possesses the most external variation recognized in *Adelops.* The variation has led to the previous creation of three other specific names. I treat the variation as being within one species because of the uniformity of the internal male and female characters which I believe are better characters upon which to base species recognition.

Greatest noticeable variation is in the elytral striae. In all California material and most of that from the southwestern states, the striae are distinctly transverse to the elytral suture. Material from the Pacific Northwest possesses striae that range from being distinctly oblique to the suture to slightly oblique. Within one population, such as that from Creston, British Columbia, there is a relationship between striae and body width, with the broader individuals possessing striae that are more distinctly transverse. Throughout the range, the larger specimens are generally with finer and more transverse striae.

Using the external characters, the northwestern populations generally can be easily distinguished from those at the southern and eastern edges of the species range. However, geographically intermediate populations are also intermediate in external characters. This, combined with the uniformity of the genitalia, is my reason for uniting the various populations into one species. This problem of taxonomy and variation is like the complex case of *P. subvillosus* in Europe (Sokolowski, 1956).

I have not adequately solved the problem of this variation. Much opportunity remains for additional collecting to observe the patterns of variation. If future studies show that the Pacific Northwest entities with more coarse and oblique striae merit separate taxonomic recognition, it should be either as the subspecific or specific name of *piperi,* because this is the oldest name applicable to these populations.

Other variation is minor. The Mexican population has aedeagi that are thicker in lateral view, and in a dorsal view at the tip, and spermathecae that are thinner and have a slightly smaller anterior end. The spermatheca differs in the same way in Mojave Desert material, and the spiculum is more than 1/2 free from the genital plates. The aedeagus of Medicine Hat, Alberta, males is less elongate and less hooked at the end.

Field notes. Most of the habitat records for the species indicate that it is an inhabitant of nests and burrows of small mammals. It is known from pocket gopher nests in California, Texas (Ross, E. S., 1944), Kansas, North Dakota, British Columbia, and Durango, Mexico; from mouse nests in Utah and California; *Dipodomys* nests in California; marmot burrows in British Columbia; spermophile nests in Alberta and British Columbia; and *Speotyto* (burrowing owl) nests in Washington and Idaho. One was taken from a shelf fungus in California; one at a light in Kern County, California, and one in a malt trap in British Columbia.

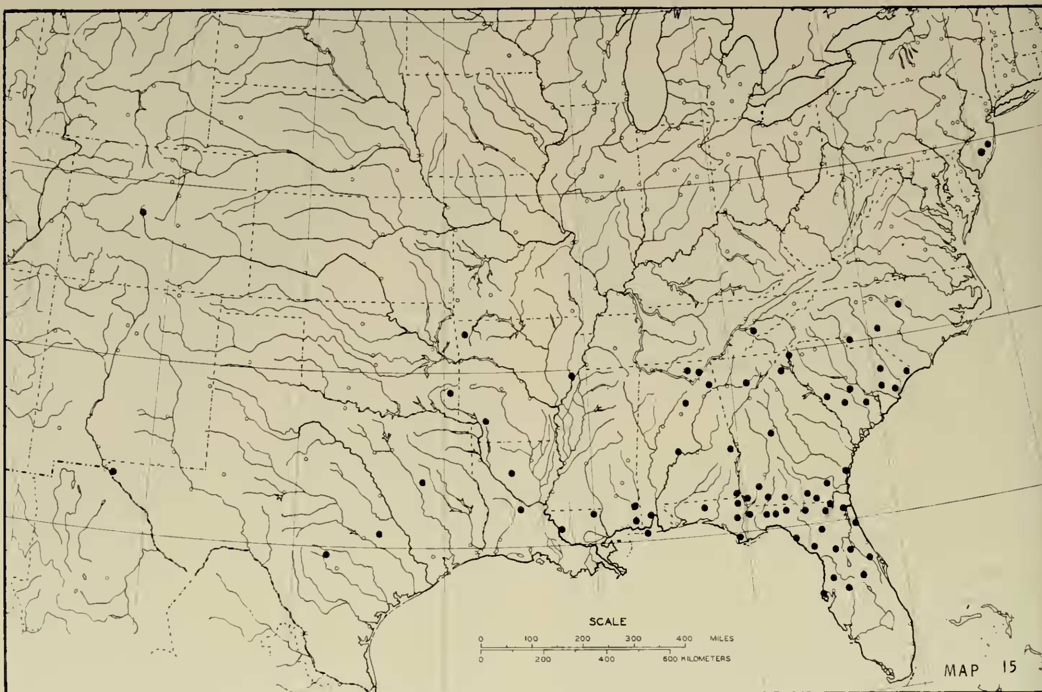
Seasonality. Little seasonality would be expected for individuals living in protected

nests and burrows. Adults have been collected in every month except August. The greatest numbers are from winter month collections in California, and spring and early summer collections elsewhere. Larvae are unknown.

Distribution. This species has the widest range of any known *Adelops.* It is distributed in southern Canada from British Columbia eastward to Manitoba, and southward through the prairie and mountain states to Texas and California, with one known Mexican population. I have seen 431 specimens from the following localities:

CANADA. ALBERTA. Medicine Hat (spermophile hole), 2 (CAS); Whitford Lake, 1 (CAS). BRITISH COLUMBIA. Creston (47 in gopher burrow, Stace Smith leg; and 16 in *Citellus* burrows), 27 (MCZ, CNCI, CAS, UBCZ); Osoyoos (8 mi. E), 3 (CNCI). MANITOBA. Treesbank, 3 (CNCI). **MEXICO.** DURANGO. El Salto (10 mi. W, 3 in gopher burrow), 13 (CNCI); El Salto (11 mi. SW), 6 (CNCI). **UNITED STATES.** ARIZONA. *Pima County:* Santa Catalina Mts., 5 (CAS, MCZ). *Yuma County:* Yuma, 2 (INHS). CALIFORNIA. *Alameda County:* Castro Valley (gopher nest), 2 (CAS); no locality, 7 (CAS). *Contra Costa County:* Antioch (gopher burrow), 3 (CAS); Danville (18 in gopher nest under board, 2 in debris of ground nest of *Vespula* wasp, 111 in gopher [*Thomomys*] nest, 4 in gopher burrow) (CAS); Mt. Diablo (1800′, field mouse nest), 1 (CAS); Vine Hill, 1 (CAS). *Fresno County:* Fresno, 1 (USNM); Coalinga, 1 (CUIC). *Kern County:* Alta Sierra (5800′, light), 1 (CNCI). *Kings County:* Hanford (shelf fungus), 1 (CNCI). *Lake County:* Blue Lake, 1 (CAS). *Los Angeles County:* Little Rock (Mojave Desert, *Dipodomys* nest), 6 (CAS); Pasadena, 5 (CAS, MCZ); Los Angeles, 1 (USNM). *Marin County:* Novato (*Thomomys* nest), 23 (CAS). *Monterrey County:* Carmel, 3 (CAS, CUIC). *Orange County:* Cypress, 1 (USNM). *Riverside County:* Colton, 1 (INHS); San Jacinto, 1 (USNM). *San Bernardino County:* Victorville (mouse nest), 4 (AMNH). *San Diego County:* Poway, 3 (MCZ, CAS); San Diego, 3 (CAS); Sta. Ysabel, 1 (MCZ Leconte); Jct. to Vallecitas (rodent burrow), 1 (CAS); Trib. to Jamul Cr. near Lower Otay Lake (flood debris), 1 (CAS). *San Francisco County:* San Francisco, 2 (USNM); Lake Merced, 3 (CAS); Presidio (*Thomomys* burrow), 1 (CAS); San Miguel Hills (San Francisco), 1 (CAS). *San Mateo County:* Salada Beach, 1 (CAS); Stanford University, 1 (USNM). *Tehama County:* Red Bluff, 13 (CAS). COLORADO. *Clear Creek County:* Georgetown (8300′–8600′), 1 (USNM). *Denver County:* Denver, 2 (USNM). *Grand County:* Grand Lake, 1 (CAS). *Moffat County:* Craig, 1 (CNCI). IDAHO. *Bingham County:* No locality (*Speotyto* nests), 6 (USNM). KANSAS. *Douglas County:* No locality, 1 (SEMC). *Saline County:* Salinas (*Geomys bursarius* burrow), 3 (CAS). NEVADA. *Esmeralda County:* Goldfield, 11 (CAS, USNM Casey coll., FMNH, MCZ, CNCI). NORTH DAKOTA. *Ransom County:* McLeod (5 mi. SW, *Geomys* burrow), 2 (CNCI). OREGON. *Baker County:* Spring Creek, 1 (GHNC). *Klamath County*: No locality, 1 (FMNH). TEXAS. *Bexar County:* Sommerset (*Geomys bursarius* burrow), 3 (CAS). *El Paso County:* El Paso, 2 (MCZ). UTAH. *Garfield County:* Hanksville (24 mi. S, 7500′), 2 (CNCI); Lonesome Beaver (7500′, mouse nest), 16 (CNCI). *Morgan County:* Strawberry Res. (SE of Ogden, 8000′), 3 (CAS). WASHINGTON. *Adams County:* No locality (*Speotyto* nests), 3 (USNM). *Douglas County:* No locality (*Speotyto* nests), 8 (USNM). *Franklin County:* No locality (*Speotyto* nests), 12 (USNM). *Garfield County:* Pullman, 2 (USNM). *Okanogan County:* No locality (*Speotyto* nests), 17 (USNM). *Walla Walla County:* College Place, 1 (GHNC). *Yakima County:* No locality (*Speotyto* nests), 5 (USNM).

Distributional comments. Hatch (1957:



Map 15. Distribution of *Ptomaphagus (Adelops) consobrinus.*

42) reports as *thomomysi* what may be this species from Corvallis (*Peromyscus* nest) and Medford, Oregon.

Ptomaphagus consobrinus (Leconte)
Figures 1, 4, 52, 53, 94, 125, 178, 179, 206; Map 15

Catops consobrinus Leconte, 1854: 281. Lectotype here designated as female in MCZ (Leconte coll.) bearing red label "type 3151," with a printed label "Ga," and a hand written label "N. Orleans Motsch," seen. Published type locality: Georgia.

Catops strigosus Leconte, 1854: 281. Lectotype here designated as female in MCZ (Leconte coll.) bearing red label "type 3152" and a small white paper square (meaning eastern United States in Leconte's locality code), and a rectangular yellow label marked "7562," seen. Published type locality: South Carolina.

Catops lecontei Murray, 1856: 459. Name proposed for *C. strigosus* Leconte, type and locality the same.

Ptomaphagus consobrinus Leconte, Horn, 1880: 263; Hatch, 1933: 206.

Ptomaphagus (Adelops) consobrinus Leconte, Jeannel, 1936: 92; 1949: 98.

Ptomaphagus (Adelops) carolinensis Schweiger, 1949: 1. Holotype male and allotype female in Reichsmuseum, Stockholm, seen. NEW SYNONYMY. Type locality: South Carolina.

Diagnosis. This species is found only east of the Rocky Mountains in Canada and the United States. Its large eyes and dark color separate it from all eastern species except *brevior* and *ulkei* and it is separated from these by the shape of the spermatheca, the long, thin, curved aedeagus, and the genital segment with a long spiculum and genital plates that are both elongated anteriorly and notched on the border of the orifice.

Description. Length 2.5–3.2 mm. Width 1.2–1.5 mm. Color dark brown to piceous. Head pubescent, punctured. Eyes normal, their horizontal diameter 2.2 times width of space between their anterior margin and antennal socket. Antennae (Fig. 125)

short, not reaching edge of pronotum when laid back; segments II and III longer than broad, IV and V subquadrate; VI–X distinctly transverse. Pronotum widest at base; sides parallel behind; 1.5 times as wide at base as long; hind margin curved; elytra 1.4 times as long as wide at base, slightly wider 1/3 behind base; female apex obliquely truncate, very slightly drawn out at suture; male apex transversely rounded. Mesosternal keel (Fig. 94) low, notch present. Aedeagus (Fig. 52) regularly curved, long, thin; tip pointed; in dorsal view tip rounded with tooth (Fig. 53). Genital plates (Fig. 206) elongated anteriorly along spiculum gastrale, 2/3 enclosing long thin spiculum; slight concavity in edge bordering genital orifice (arrow in Fig. 206). Spermatheca (Figs. 178, 179) thin, very twisted; anterior end thin, not swollen or flattened in side view.

Variation. The variation in the species is slight. Some variation occurs in the spermatheca when ends of the range are compared (Figs. 178, 179). The spermatheca of the lectotype of *P. strigosus* (Leconte) (=*lecontei* Murray) is identical to that of the lectotype of *consobrinus*. By its description and illustrations it is inseparable from *consobrinus*, which is the only species known from South Carolina, with the exception of one specimen of *P. cavernicola*.

Field notes. The species has been frequently collected on the Coastal Plain in the southeast by using Berlese funnels. In Florida and adjacent states, W. Suter has found specimens in tree forks, tree holes, pine and oak buttresses, log and leaf litter, and palmetto debris. An Alabama collection was from fungus. Malt traps set for scarab beetles have taken large numbers in several Florida localities as well as in North and South Carolina and Georgia. It can be only occasionally taken at carrion, but four traps in Torreya State Park, Florida, captured 42 in a week in early April. A long-term carrion study in South Carolina by Payne and King (1970) found only this species of *Ptomaphagus*, and this only infrequently. Gopher tortoise burrows in Florida yielded two specimens that I have seen (see field notes of *P. texanus* for additional data on tortoise burrows). A. Newton, using human dung and rotted squid as bait in pitfall traps, has taken this species often in pine-oak woods in New Jersey. Additional habitat documentation is found in the distribution section.

Seasonality. Adults have been taken in every month of the year. The winter month collections are from the more southern localities and are mostly from malt traps and litter. Early spring to early summer months probably represent the period of greatest activity since the largest collections are made at this time, usually in baited traps. Nothing is known about reproductive seasonality, but it seems that most reproduction would occur in the spring. Only a few larvae are known from Berlese funnel collections.

Distribution. The species is distributed in the southern Gulf Coastal Plain states from Texas to Florida, northward to Colorado and the pine barrens of New Jersey. I have seen 1356 specimens from the following localities:

ALABAMA. *Blount County:* Inland Lake (rock crevice debris), 1 (FMNH). *Dallas County:* Selma, 3 (USNM). *DeKalb County:* Ft. Payne (in cave), 14 (UANH). *Houston County:* Gordon (log with polypore), 1 (FMNH); Chattahoochee St. Park, 1 in sassafrass tree hole, 3 in 139 lbs. log litter (FMNH, SBP). *Jackson County:* Scottsboro (forest carrion trap), 1 (SBP). *Madison County:* Monte Sano, 2 (HAHC). *Mobile County:* Mobile, 10 (CUIC, UANH); Spring Hill (in fungus), 4 (UANH). Dauphin Island, 7 in pine tree fork, 3 in magnolia tree hole (FMNH). *Russell County:* Seale, 5 (HAHC). ARKANSAS. *Hempstead County:* Hope, 1 (MCZ). *Phillips County:* Helena, 1 (USNM). *Washington County:* No locality, 5 (INHS). COLORADO. *Denver County:* Denver, 1 (USNM). FLORIDA. *Alachua*

County: High Springs (4 mi. N, malt-proprionic acid traps), 15 (HAHC, FSCA); Archer, 28 (CNCI); Gainesville (10 on carrion, 24 in malt traps), 37 (CNCI, FSCA, USNM, PURC); Newnans Lake (malt traps), 31 (FSCA). *Baker County:* McClenny (5 mi. N), 19 in palmetto debris, 14 in bush fork, 229 in malt traps (SBP, FMNH, FSCA); Glen St. Mary (malt trap), 97 (FSCA). *Calhoun County:* Clarksville (1 at light, 1 in malt trap), 12 (HAHC, MCZ); Scotts Ferry (oak litter), 2 (FMNH). *Columbia County:* Suwannee River (pine buttress), 1 (FMNH). *Dixie County:* Steinhatchee, 1 (CNCI). *Duval County:* Jacksonville, 1 (USNM). *Gulf County:* Honeyville (1 at oak log, 3 at pine buttress) (FMNH); Wewahitchka (edge sawdust pile), 8 (FMNH). *Hernando County:* Brooksville (Anataloga Hammock, 1 at log, 5 in maple duff, 1 at oak buttress) (FMNH). *Jackson County:* Florida Caverns St. Park (forest carrion traps), 4 (SBP). *Jefferson County:* Capps (pine buttress), 4 (FMNH); Wacissa (pine buttress), 1 (FMNH). *Lafayette County:* Branford (12.8 mi. NW, malt traps), 2 (FSCA). *Leon County:* Tallahassee, 3 (HAHC); Iamonia (beech log), 17 (FMNH); Woodville (sweetgum litter), 4 (FMNH); Chavies, 5 in pine buttress, 3 in fibrous floor litter (FMNH); Silver Lake (pine buttress), 5 (FMNH); Tallahassee, 2 in gum log, 4 in pine stump, 2 in magnolia bush fork (FMNH). *Levy County:* Bronson (pine-maple pseudofork), 18 (FMNH); Coes Landing (log), 1 (FMNH); near Bronson and "area 3" (malt traps), 19 (FSCA); no locality, 37 (MCZ, CAS, CNCI). *Liberty County:* Torreya St. Park (42 in carrion trap, 1 in 185-liter log Berlese, 10 in malt trap), 53 (SBP, FSCA). *Madison County:* Madison (floor at log), 2 (FMNH). *Marion County:* Ocala (14.5 mi. E, malt), 3 (HAHC); Silver Springs (palm stump), 6 (FMNH); no locality, 3 (MCZ, CNCI). *Orange County:* S. Orlando (pine-cypress stump debris), 1 (FMNH). *Pinellas County:* Dunedin, 38 (TAMU, CUIC, PURC, AMNH, CAS, MCZ); Coachman, 3 (CUIC). *Polk County:* Lakeland, 1 (PURC). *Putnam County:* Crescent City (gopher hole), 2 (USNM); Welaka (Univ. Florida Conserv. Reserve, malt traps), 305 (FSCA). *St. Johns County:* St. Augustine, 2 (MCZ). *Volusia County:* Enterprise, 1 (MCZ). *Walton County*: DeFuniak Springs (dead owl), 4 (HAHC). GEORGIA. *Baker County:* Newton (Emory Univ. Field St., malt traps), 3 (HAHC). *Brantly County:* Nahunta (oak tree crotch), 2 (FMNH). *Brooks County:* Quitman (pine buttress), 2 (FMNH). *Charlton County:* St. George, 5 at log, 1 in magnolia litter, 1 in sawdust, (FMNH). *Clinch County:* Dupont (sawdust under ferns), 2 (FMNH). *Echols County:* Needmore (pine buttress), 4 (FMNH). *Glynn County:* Thalman (pine-oak tree crotch), 2 (FMNH); Jekyll Island (palmetto axil), 1 (FMNH); Brunswick, 1 (USNM). *Grady County:* Calvary, 2 in *Cornus* stump and 1 in pine-sweetgum tree fork (FMNH); Beachton (oak branch litter), 1 (FMNH). *Peach County*: No locality, 1 (USNM). *Seminole County:* Donaldsonville (pine buttress), 2 (FMNH). *Stephens County:* Toccoa (5 mi. W), 1 (CNCI). LOUISIANA. *East Baton Rouge Parish:* Baton Rouge, 1 (USNM). *Rapides Parish:* Alexandria (10 mi. SW), 26 (CNCI). *Washington Parish:* Bogalusa, 2 (USNM, CUIC). *Winn Parish:* Winnfield, 1 (MCZ). MISSISSIPPI. *George County:* Lucedale, 3 (CUIC). *Jackson County:* Lakehurst, 25 (AMNH). *County not located:* Manchester, 2 (CNCI). NORTH CAROLINA. *Moore County:* Southern Pines (12 at malt traps), 23 (CNCI, HAHC, MCZ, USNM Casey coll.). *Union County:* No locality (woods trash), 1 (USNM). *Wake County:* Raleigh (4 at carrion), 5 (HAHC). OKLAHOMA. *Leflore County:* Heavener (10 mi. SW, Winding Stair Watchtower, log litter), 2 (SBP). SOUTH CAROLINA. *Aiken County:* Graniteville (malt traps), 37 (FSCA); Aiken (malt), 25 (HAHC, FSCA). *Bamberg County:* Bamberg (woods

Map 16. Distribution of *Ptomaphagus* (*Adelops*) *brevior*.

trash), 2 (VMKC). *Calhoun County*: No data, 1 (SBP). *Dorchester County*: No locality, woods trash, 2 (VMKC). *Florence County:* Florence (5 in woods trash, 1 in field corn ear, 1 in broom sedge), 20 (VMKC, CNCI, MCZ). *Georgetown County*: No locality, 2 (SBP). *Horry County:* Little River (woods trash and broom sedge), 3 (VMKC). *Pickens County:* Clemson (Payne carrion study), 4 (SBP); Greenville (woods trash), 1 (VMKC). *Williamsburg County:* Kingstree (malt), 1 (HAHC); No locality, 1 (NR) (type male *Pt. carolinensis*). TENNESSEE. *Blount County:* Chilhowee Mt. (malt), 1 (HAHC). TEXAS. *Anderson County:* Elkhart (10 mi. SW), 3 (TAMU). *El Paso County:* Fabens (light), 1 (HAHC). *Lee County:* Fedor (an old locality?), 5 (MCZ, USNM, CAS). *Kerr County*: Kerrville (malt traps), 3 (CNCI).

Ptomaphagus brevior Jeannel

Figures 54, 55, 95, 122, 180–184, 207; Map 16

Ptomaphagus (*Adelops*) *brevior* Jeannel, 1949: 98. Holotype male in MNHN, seen. Type locality: Indiana, Putnam County.

Diagnosis. This species is widespread in the eastern United States, especially in the more northern states. Its range, piceous

color, short antennae, and large eyes separate it from all other species except *ulkei* and *consobrinus*. Its deeper and more rounded mesosternal notch, concave margin of the male genital segment, and shorter, thicker aedeagus separate it from *consobrinus*. Its longer aedeagus and broader genital plates separate it from *ulkei*. It is separated from all other species by the shape of the female spermatheca.

Description. Length 2.4–3.1 mm. Color dark brown piceous, antennal base lighter. Head finely punctured, pubescent. Eyes with horizontal diameter 2.8 times width of space between their anterior margin and antennal socket. Antennae (Fig. 122) short, not reaching base of pronotum when laid back; segments II–III longer than broad, IV–X broader than long. Pronotum 1.5 times as wide at base as long, slightly wider 1/3 before base; hind margin slightly sinuous; elytra 1.5 times as long as wide; apex rounded-obliquely truncate in male; obliquely truncate in female, edge not sinuous at suture. Mesosternal notch (Fig. 95) usually very well developed, deep, rounded. Aedeagus (Fig. 54) curved, broader at base, tapering to point with down-curved tooth; in dorsal view (Fig. 55) broadly rounded with terminal tooth. Genital plates broad, anteriorly projected along and 3/4 enclosing long thin spiculum (Fig. 207). Spermatheca variable (Figs. 180–183), central shaft curved, posterior end curved back on itself and usually broadly flattened, anterior end broadly flattened.

Variation. This species has the greatest variation in the spermatheca of any known epigean *Adelops*. The variation is most evident in Texas when eastern localities (Brazos, Colorado, Dallas counties) are compared with central (Bexar, Gonzales) localities. In Bexar and Gonzales County females the spermatheca is smaller and more compact (Figs. 182, 183). Colorado County spermathecae (Fig. 180) are intermediate in shape. The common shape (Fig. 181) is constant throughout the rest of the species' range. Insufficient material is available to determine if the change in spermathecal form in Texas is gradual or sharp. The nature of this variation can be studied only after additional extensive collecting.

This species presented the only recognized case of teratological variation in the spermatheca. This was in one specimen from Round Knob, North Carolina (Fig. 184). Two other specimens from this locality were normal.

All the Texas populations are different in the form of the mesosternal notch, which resembles that of *consobrinus* in that it is not deeply incised and rounded.

Field notes. Most collections are of a few specimens only. They have been taken in Berlese samples and by sifting litter in Ontario, Massachusetts, Texas, and Illinois; in human dung-baited pitfall traps in Texas and Massachusetts; and at carrion in Alabama, Illinois, Kentucky, Massachusetts, Michigan, Missouri, and New York. In Massachusetts they have also been taken in traps baited with skunk cabbage leaves.

Seasonality. Specimens have been collected in every month except February and December. Records for January and November are from Texas. Records for July and August are from high elevations in Tennessee and North Carolina. The one September record was from a litter sample in New York. The bulk of the specimens were collected from March to June. In Massachusetts trapping by Al Newton and myself showed that the beetles are active from early March until June, and are not trapped in the summertime.

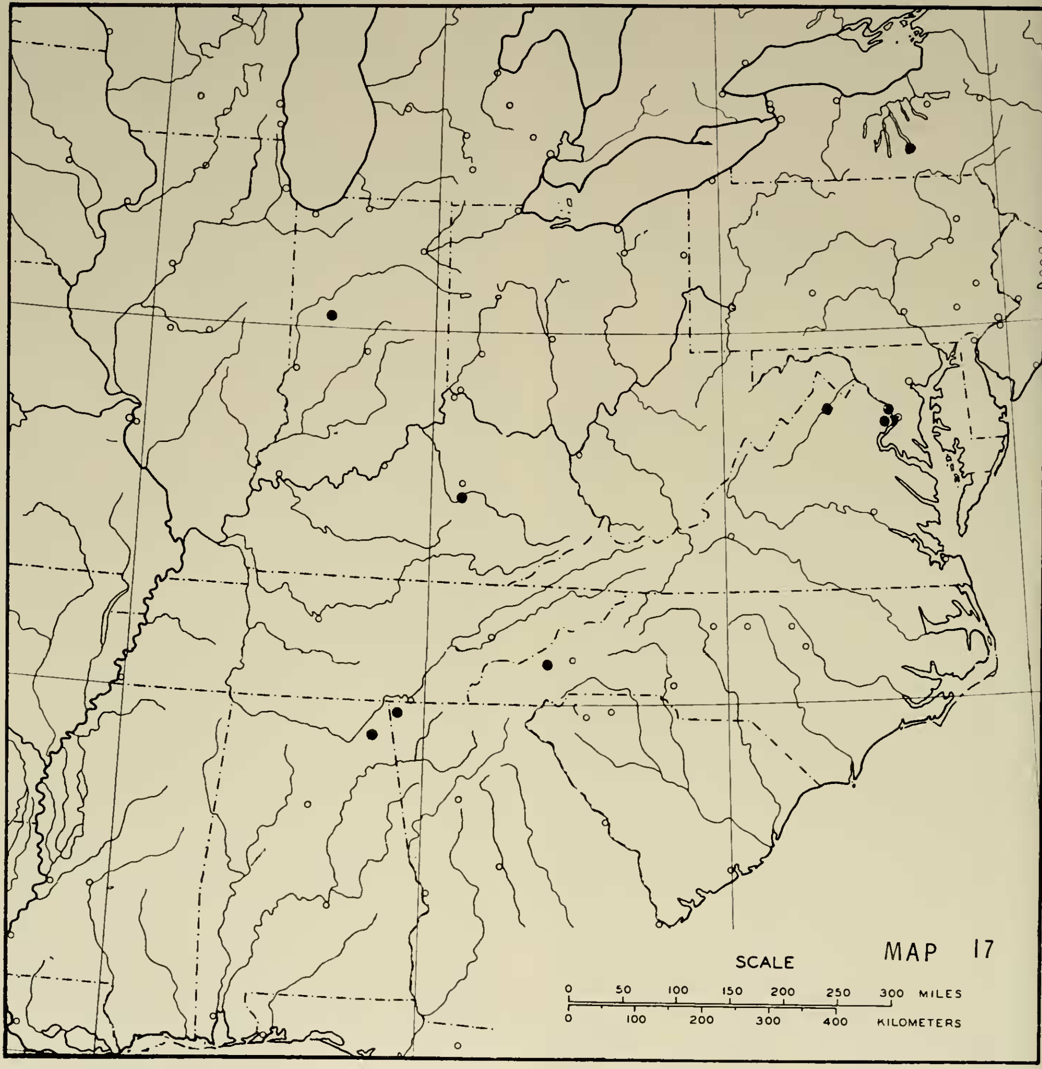
Reproduction is known to occur only in late spring but may occur earlier. Adult females captured in May in Massachusetts produced eggs only until late May, and then died. Males lived until mid-July. Additional data on reproduction will be in a separate paper on the life cycles of *Ptomaphagus*.

Distribution. The species ranges from southern Quebec and southern Ontario,

southward through most of the glaciated eastern United States to the southern Appalachians, with a series of peripheral and variant populations in Texas. It is known on the Coastal Plain only in Texas. I have seen 195 specimens from the following localities:

CANADA. ONTARIO. Ancaster, 3 (CNCI); LaSalle (sifting), 9 (KS); Maidstone, 3 (KS); Tillsonburg, 1 (CNCI). QUEBEC. Rigaud, 4 (CCC). **UNITED STATES.** ALABAMA. *Jackson County:* Scottsboro (forest carrion trap), 1 (SBP). *Madison County:* New Market (4 mi. E, carrion trap), 1 (SBP). CONNECTICUT. *Litchfield County:* Washington, 1 (FMNH). *New Haven County:* New Haven, 1 (MCZ). DISTRICT OF COLUMBIA. Washington, 1 (USNM). GEORGIA. *Rabun County:* Clayton (2000–3700 ft.), 1 (CNCI). ILLINOIS. *Cook County:* Des Plaines (Carle Woods, carrion), 17 (SBP). *DuPage County*: Argonne National Lab., 9 (traps) (FMNH). *St. Claire County:* no locality, 1 (FMNH). *Will County:* Joliet, 1 (FMNH). INDIANA. *Posey County:* no locality, 1 (PURC). *Putnam County:* no locality, 2 (PURC, MNHN). IOWA. *Jackson County:* Maquoketa Caves St. Park (Berlese, 297 lbs. leaf litter), 1 (SBP). *Johnson County:* Iowa City, 1 (USNM). KENTUCKY. *Carter County:* Carter Caves St. Park (molasses trap), 1 (SBP). *Harlen County:* Pine Mt. (2 at carrion trap, 4000′), 5 (SBP, ANSP). MARYLAND. *Montgomery County:* Plummers Island, 9 (USNM). MASSACHUSETTS. *Middlesex County:* Cambridge, 2 (MCZ, USNM); Framingham, 1 (MCZ); Lincoln (forest carrion trap), 1 (SBP); Medford (Middlesex Fells Res., carrion and human dung traps), 30 (SBP); Natick, 1 (HAHC); Sherborn, 2 sifting, 1 sweeping, 2 skunk cabbage traps, (MCZ, NYSM); Stoneham (Middlesex Fells Res., carrion, skunk cabbage, and human dung traps), 24 (SBP); Winchester, 2 at human dung (SBP). *Suffolk County:* Dorchester, 1 (MCZ). MICHIGAN. *Barrien County:* Warren Woods (carrion traps), 2 (SBP); Mud Lake Bog (carrion trap), 3 (SBP). *Clinton County:* Rose Lake (pitfall traps), 5 (SBP). *Oakland County:* No locality, 1 (MCZ). *Wayne County:* Detroit, 9 (ANSP, USNM). MISSOURI. *Jefferson County:* High Ridge (sinkhole forest-carrion trap), 18 (SBP). *St. Charles County:* No locality, 3 (MCZ). NEW YORK. *Bronx County:* Bronx Park, 4 (USNM). *Erie County:* Buffalo, 2 (CAS). *Monroe County:* Rochester, 1 (SBP). *Niagara County:* Olcott, 1 (CUIC). *Rensselaer County:* Berlin (under board with rodent runways), 1 (SBP); Valley Falls, 1 (NYSM). *Richmond County:* Staten Island, 1 (USNM). *Orange County:* Mountainville, 1 (NYSM); West Point, 2 (USNM). *Tompkins County:* Ringwood Forest (7 mi. E Ithaca, carrion), 1 (SBP); Ithaca, 2 (CUIC). *Westchester County:* Peekskill, 1 (CNCI). *Yates County:* Penn Yan, 1 (CUIC); unlocated locality, Danby, 1 (CUIC). NORTH CAROLINA. *Haywood County:* Black Mountains (Mt. Mitchell), 7 (AMNH, CAS, MCZ); Round Knob, 3 (USNM). *Jackson County:* Whiteside Mt., 2 (TCB). *Swain County:* Great Smoky National Park (Heintooga Overlook, Mollies Gap, carrion trap, 5000′), 1 (SBP). PENNSYLVANIA. *Northampton County:* Easton, 1 (CAS). *Philadelphia County:* Frankford, 1 (USNM). *Tioga County:* Arnoto, 1 (SBP). *Westmoreland County:* Chestnut Hill, 1 (MCZ); St. Vincent, 1 (USNM). TEXAS. *Bexar County:* San Antonio, 3 (MCZ, USNM). *Brazos County:* College Station, 1 (TAMU). *Colorado County:* Columbus, 12 (USNM, CAS). *Dallas County*: Dallas, 1 (USNM); No locality, 1 (GHNC). *Gonzales County:* Palmetto St. Park, 2 in leaf litter, 2 in human dung trap, (SBP).

Distributional comments. A gap in the distribution exists between the Texas populations and those of the northern and eastern states (Map 16). Insufficient collecting has been done to state whether or not this gap is real.



Map 17. Distribution of *Ptomaphagus (Adelops) ulkei.*

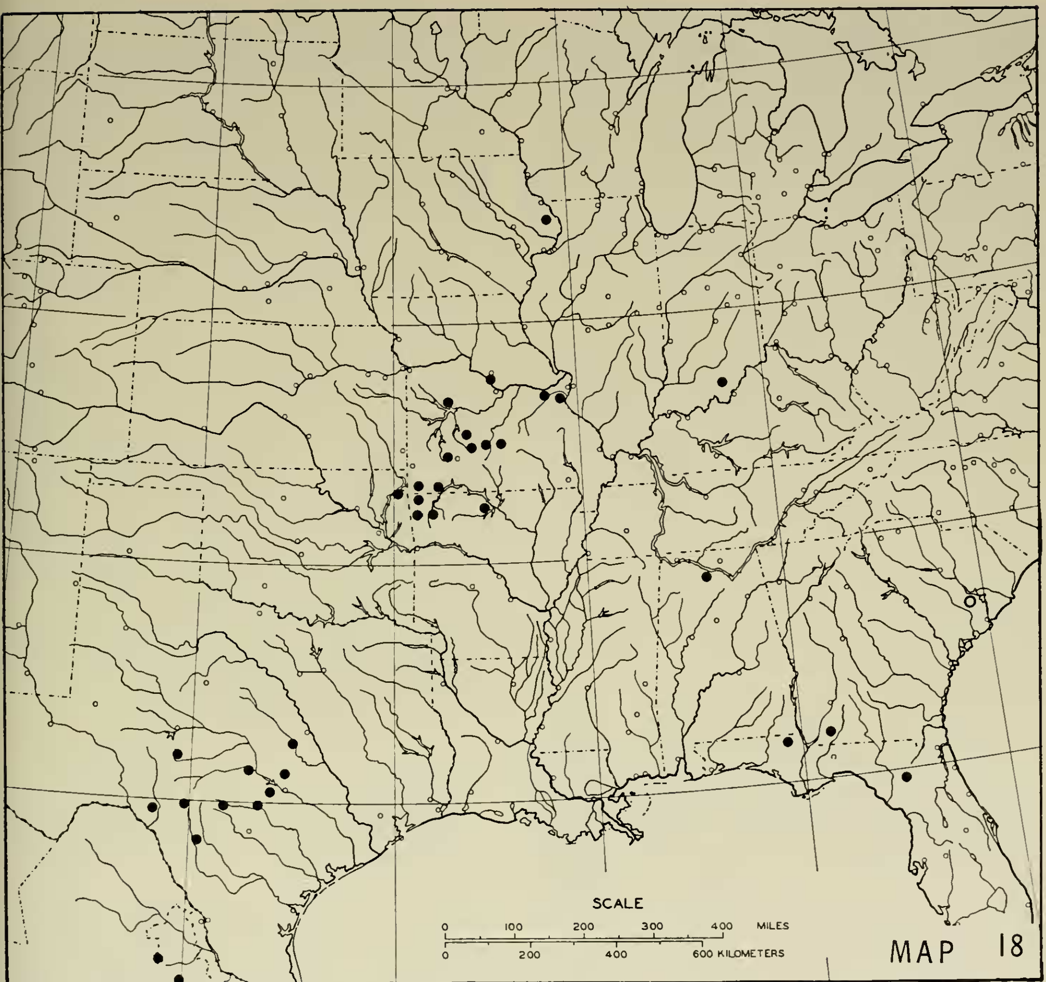
Ptomaphagus ulkei Horn
Figures 56, 57, 96, 127, 185, 186, 208; Map 17

Ptomaphagus ulkei Horn, 1885: 137. Lectotype here designated as male in ANSP (no. 2998), seen. Type locality: District of Columbia. Hatch, 1933: 205.

Ptomaphagus (Adelops) ulkei, Jeannel, 1936: 92; 1949: 98.

Diagnosis. This species is difficult to distinguish from *brevior* and *consobrinus,* which also occur in the southeastern United States. It is best distinguished by the aedeagus and unique form of the female spermatheca.

Description. Length 3.3–4.3 mm. Width 1.5–2.2 mm. Color dark brown. Head finely punctured, pubescent. Eyes normal, their horizontal diameter 3 times the width of the space between their anterior margin and antennal socket. Antennae (Fig. 127) short, not reaching base of pronotum when



Map 18. Distribution of *P.* (*Adelops*) *cavernicola*. The symbols represent only county records. This troglophilic species is known from 55 cave localities (dark circles) and one epigean locality (open circle) in South Carolina.

laid back; segments II and III longer than broad, IV–X transverse, VI–X strongly so. Pronotum widest by slight amount 1/3 before base; 1.5 times as wide at base as long; hind margin sinuous. Elytra 1.3 times as long as broad at base; apex transversely truncate and slightly rounded in both sexes. Mesosternal notch distinctly and deeply incised (Fig. 96). Legs in large males with metatibiae strongly curved, less so in smaller males. Aedeagus (Fig. 56) short, stout, curved in posterior half, tip narrow; in dorsal view tip broad with terminal tooth (Fig. 57). Genital plates elongate, enclosing 3/4 of normal spiculum (Fig. 208). Spermatheca narrow in side view (Fig. 186), in dorsal view (Fig. 185) thin, shaft curved, posterior opening facing right.

Variation. The size variation of this species is the greatest for any known *Adelops*. Some individuals are the largest specimens known for the genus in the United States. A female from Georgia

showed variation in the spermatheca in that the posterior end was more curved over in an anterior direction.

Field notes. I took four in a forested ravine at decaying fish bait in Madison County, Kentucky, and one at a carrion pitfall trap in a forested sinkhole in Georgia. A Virginia specimen was found on a dead snail. Data is not available for other specimens but they probably came from forested habitats.

Seasonality. Adults have been taken in April, May, June, July, and September, with 13 of the 21 adults being captured in May and June. Larvae are not known.

Distribution. The species is known from central New York, westward to central Indiana, and southward to northwestern Georgia (Map 17). I have seen 24 specimens from the following 11 localities:

ALABAMA. *DeKalb County:* Manitou Cave (at Fort Payne), 2 (AMNH). GEORGIA. *Dade County:* 4.5 mi. NE Rising Fawn (outside Johnson Crook Cave), 1 (SBP). INDIANA. *Montgomery County:* Crawfordsville, 1 (INHS). KENTUCKY. *Madison County:* Clays Ferry, 4 (SBP). MARYLAND. *Montgomery County:* Plummers Island (Cabin John), 9 (USNM). NEW YORK. *Tompkins County:* Six Mile Creek (Ithaca), 1 (PISZ). NORTH CAROLINA. *Haywood County:* Cosby Knob, 1 (KS); Round Knob, 1 (USNM). VIRGINIA. *Alexander County:* No data, 2 (USNM). *Fairfax County:* Dead Run, 1 (USNM). *Warren County:* Limeton (on dead snail), 1 (USNM).

The *Cavernicola* Group

Diagnosis. Spermatheca shaped like a reversed "S" in anterior end but with posterior end curved around in a coil and then bent to the left; anterior end expanded and flattened (Figs. 187–197).

Description. Shape elongate oval. Color light to dark brown. Eyes large to reduced, pigmented or unpigmented. Antennae short to long. Pronotum with hind angles acute, striae distinct. Elytra with external angles rounded, apex oblique or rounded-truncate in females, and rounded in males; sutural angles of females rounded or sharply acute; some female elytral tips with pruinose area. Wings normal or reduced. Mesosternal carina medium or low. Legs normal or elongated. Aedeagus elongate, gently curved; pointed at tip in lateral view; dorsal view of tip pointed to broad.

The group contains ten named species and seven recognized but unnamed species. All but one of the above are limited in distribution to Mexico and Guatemala. The exception is the troglophile *cavernicola,* which ranges from northeastern Mexico into and across much of the central and southern parts of the eastern United States. Two subspecies are recognized. Of the named species, two troglobites and two troglophiles are known from Mexico. The remaining five are epigean in middle- and high-elevation Mexican forests.

Ptomaphagus cavernicola cavernicola Schwarz

Figures 58, 59, 97, 126, 187–189, 209; Maps 13, 18

Ptomaphagus cavernicola Schwarz, 1898: 57. Type in USNM (No. 1424), seen. Type locality: Missouri, Stone County, Marble (=Marvel) Cave. Hatch, 1933: 204.

Ptomaphagus (*Adelops*) *cavernicola,* Jeannel 1936: 92; 1949: 101; Sanderson, 1939a: 117; Barr, 1963: 54; Peck, 1970b (Florida records).

Diagnosis. The large size and large eyes, elongate antennae with segments III–VII longer than wide and IX–X quadrate, produced female elytral tips, and the thin and twisted spermatheca serve to distinguish this cave-inhabiting species, which ranges from northeastern Mexico to the Ozarks of the United States and southeast to Florida. Antennal segments II and III are subequal, separating it from *oaxaca* which has II distinctly shorter than III. The eyes are larger in *oaxaca.*

Description. Length 3.0–4.0 mm. Width

1.4–1.7 mm. Color piceous to brown, head blackish, mouthparts and basal half of antennae testaceous. Head very finely, not densely punctate; eyes large, width of head from antennal base to margin, across eye, 1.7 times width of eye; width of eye 2.0–2.9 times width of space between antennal base and front margin of eye (except in Cueva de la Boca population with smaller eyes). Antennae (Fig. 126) slender and distinctly longer than head and thorax; segments II and III each nearly three times longer than wide; IV, V, and VI sequentially decreasing in length but VI still slightly longer than wide; VII longer than wide; VIII slightly narrower than the adjoining segments and half the length of VII; IX and X quadrate; terminal segment longer than wide, acuminate. Prothorax at base 1.4–1.7 times wider than long; slightly wider 1/3 before base; sides arcuately narrowing in front, nearly straight behind; hind margin slightly sinuate; surface transversely strigose and extremely finely punctulate, the striae much finer and denser at the sides than in the middle. Elytra at base as wide as thorax; 1.6 times as long as wide at base; gradually narrowing to apex; external apical angles more rounded in males than in females; females with acute (but not sharp) sutural angle and oblique apex. Wings normal, their length 1.6 times length of elytra from base to tip in Florida populations. I have observed them functioning in flight only in the Florida populations. Mesosternal carina low, notch conspicuous (Fig. 97). Aedeagus (Fig. 58) thickest in middle, narrowing gently to both ends, more curved in anterior end; left edge of tip raised in side view; gently tapering to apex in dorsal view (Fig. 59). Spiculum gastrale (Fig. 209) long and thin, half enclosed by genital plates that are slightly produced anteriorly. Spermatheca (Figs. 187–189) completing full spiral, small knob on posterior end; broad and flattened knob on anterior end when viewed from side (Fig. 189) and thin in dorsal view (Figs. 187, 188).

Variation. A species having this wide a range and which is apparently restricted to caves could certainly be expected to have variation. However, none of a major extent has been noted except the variation in eye size, which is used to characterize the subspecies *cavernicola aditus.* No difference was found in a study of the measurements and proportions of pronotal and elytral lengths and widths in a series of selected populations. Careful examination of aedeagi and spermathecae from many populations throughout the range showed no differences except in aedeagal mean length. Populations from Missouri and Texas have an aedeagus with a mean length of 1.26 mm (1.20–1.30 mm, n = 32). The Mexican population in Gruta Palmito has a mean aedeagal length of 1.04 mm (1.01–1.12 mm, n = 26). Alabama and Florida populations have a mean of 1.08 mm (1.04–1.12 mm, n = 11). The ranges of the aedeagal lengths of the Texas-Missouri group of populations do not overlap with the ranges of the Mexican or Alabama-Florida populations. These last two groups do overlap. I do not see any obvious evolutionary meaning or adaptive significance in this aedeagal length variation.

However, obvious evolutionary significance does occur in variation in the size of the eyes. In all populations, except that in Cueva de la Boca, the eyes are large, with an eye width of 2.0–2.9 times the width of the space from the anterior margin of the eye to the edge of the antennal socket. The eyes are reduced in the Cueva de la Boca population, which has eyes with a width of 1.5–1.75 times the width of the space between the anterior eye margin and the antennal socket. This population is formally treated below as a distinct subspecies. This one feature strongly suggests that the Cueva de la Boca population has been isolated for some time from the other populations of the species. The Cueva de la Boca population may be cave-limited, and selection for

large eyes has either been relaxed, or active selection is tending to reduce the eyes. In either case, genetic resistance to the reduction has not been recently provided by interbreeding with large-eyed populations. As a corollary to this, in all other populations of the species, either active or relaxed selection is not reducing the eyes, because the beetles are not cave-limited, or the cave limitation is so recent that not enough time has elapsed for morphological differentiation to appear.

That the species is not cave-limited in the southeastern United States is suggested by the single January collection of one female from litter in South Carolina, a state entirely free of caves.

Collecting notes. Barr (1963) reported the species from raccoon feces and dead bats. I have taken it on human dung and in bat guano in Texas, Florida, and Mexico. I have baited and trapped it with both carrion and human dung in Florida and Ozark caves. Sanderson (1939a) reported the beetles in Arkansas by the hundreds, where they crawl "over the cave floor, in bat guano and raccoon dung, in decayed vegetable debris washed and carried into caves, and . . . . to ground beef and banana peel when allowed to decay." It can also be found on old moist cigarette and cigar butts left in caves. Occasional lone specimens are found in debris and under rocks. The one specimen from an epigean locality was taken from woods trash in late January in South Carolina.

Seasonality. The species seems not to be seasonal, but to be active and breeding all year round. Barr (1963) collected larvae in January in Missouri. Another Missouri population was found in January exposed to a cold, dry current of air blowing in from a cave entrance. Florida, Ozark, and Texas collections have been made in both winter and summer months. The Mexican populations have been collected only in March and June. A few populations may have seasonality of some sort. In June 1964 I took 63 individuals in Devils Sinkhole, Texas, but in February 1965 James Reddell could find none.

Distribution. The nominate subspecies is known from 55 cave localities and one epigean site. It ranges from Florida, South Carolina, and Alabama, to the Ozarks and Iowa, southwestward to Texas and Mexico (Maps 13, 17). Localities for the Ozarks are given in Barr (1963), most of which are included below. I have seen 845 specimens from the following 56 localities:

MEXICO. NUEVO LEÓN: La Gruta Palmito (near Bustamante, W of Sabinas Hidalgo), 45 (SBP). **UNITED STATES.** ALABAMA. *Morgan County:* Inge Cave, 1 (2.v.1959, T. Barr) (TCB); Talucah Cave, 12 (19.vi.1942, W. B. Jones) (UANH). ARKANSAS. *Benton County:* Cave Spring Cave (Keith Lake Fish Hatchery), 7 (SBP); Tom Danford Cave, 1 (INHS). *Madison County:* Dinneys Cave (Huntsville), 6 (USNM). *Stone County:* Rowland Cave (Fifty-Six), 2 (SBP). *Washington County:* Carroll Cave, 2 (INHS); Devils Den Cave (Devils Den State Park), 1 (SBP); Finchers Cave, 2 (INHS); Granny Dean Cave (Corkscrew Cave), 299 (CNCI, FMNH, INHS, MCZ, SBP, TCB); Stephenson Cave, 5 (CNCI, MCZ). *Unknown county*: Davis Pit, 33 (SBP). FLORIDA. *Alachua County*: Warren Cave, 15 (SBP). *Jackson County*: *Millers Cave* (Florida Caverns St. Park), 201 (FSCA, SBP); Gerards Cave, 29 (SBP). GEORGIA. *Grady County*: Waterfall Cave (near Cairo), 1 (FSCA). INDIANA. "Wash. Co. Ind," 6 (CMNH), a questionable record. IOWA. *Jackson County*: Hunters Cave, 2 (SBP). MISSOURI. *Benton County:* Lish Estes Cave, 2 (SBP). *Boone County:* Devils Icebox Cave, 3 (TCB); Hall Cave, 1 (USNM); Hunters Cave (5 mi. NNW Ashland), 4 (USNM). *Camden County:* Carrol Cave, 7 (TCB). *Franklin County:* Fisher Cave, 3 (TCB). *Greene County:* Low Water Bridge Cave, 3 (SBP). *Jefferson County:* Pleasant Valley Cave, 8 (SBP); Rices Cave (3 mi. NE Goldman),

32 (USNM). *Laclede County:* Mary Lawson Cave, 2 (TCB). *McDonald County:* Henson Cave, 3 (SBP). *Phelps County:* Granny Baker Cave, 1 (INHS); Spencer Cave (7 mi. NW Rolla), 7 (TCB). *Pulaski County:* Inca Cave, 3 (TCB). *Stone County:* Dillo Cave, 1 (TCB); Fairy Cave, 2 (TCB); Marvel Cave, 16 (AMNH, USNM, TCB). *Texas County:* Bat Cave (7 mi. NE Success), 4 (USNM). SOUTH CAROLINA. *Orangeburg County:* Holly Hill, 1 (V. M. Kirk leg., woods trash, VMKC). TEXAS. *Burnett County:* Longhorn Caverns, 4 (SBP). *Comal County:* Brehmer-Heidrich Cave, 1 (SBP); Little Gem Cave, 2 (SBP). *Coryell County:* Shell Mt. Bat Cave, 2 (SBP); Tippets Cave, 1 (SBP). *Edwards County:* Deep Cave, 2 (SBP); Devils Sinkhole, 63 (SBP); Hughes Cave, 1 (SBP). *Kerr County:* Wilsons Cave, 4 (CNCI). *Schleicher County:* Ogleby Ranch Cave, 4 (SBP). *Travis County:* Tooth Cave, 1 (TCB). *Uvalde County:* North Well, 1 (SBP). *Val Verde County:* Fawcetts Cave (36 mi. N Del Rio), 1 (SBP). *Williamson County:* Chinaberry Cave, 1 (TCB); Coffin Cave, 1 (SBP); Laubach Cave, 2 (SBP).

Distributional comments. Notable disjunctions exist in the range (Map 18) of the species. Some of these are in areas with no caves, such as the region between central Texas and the Ozarks. The absence from caves in Illinois, Kentucky, and Tennessee is significant. These states have been fairly well collected for cave fauna by myself and others. This gap must be considered as real, and not an artifact of poor collecting. I have collected in 184 caves in Alabama alone, and the lack of more than two localities in this state shows the beetle to be indeed scarce there. The Iowa locality is also disjunct. This record is based on two specimens I collected in a pitfall trap in 1957. This population may no longer exist, for repeated baiting in this and other nearby Iowa caves has not led to the capture of additional specimens. The Indiana record is questionable. The specimens are old and adequate data does not accompany them.

The preference for caves must be for physiological or behavioral reasons. Dispersal by flight is possible for all populations in that they have fully developed wings, and I have seen them used in flight by the Florida populations. Only one collection is known from a noncave habitat, but we may assume that the species can now actively disperse. The one epigean collection from South Carolina was taken in late January, which may be a reflection of the activity season of the species in forests. The dispersal and cave occupation of more xeric areas such as the Edwards Plateau of Texas may date from a cooler and more moist time during or shortly after the Wisconsin glacial maximum.

Ptomaphagus cavernicola aditus new subspecies
Maps 13, 18

Holotype male and allotype female in MCZ (no. 31961). Type locality: Mexico, Nuevo León, Cueva de la Boca (near Santiago, 20 mi. SSE Monterrey). Type data: 22.vi.1969, S. & J. Peck. Paratypes: 50 with above data, 9 from same locality, 4.xii.1966, T. Raines; 15 from same locality, 22.vi.71, S. Peck and D. Bright.

Diagnosis. The subspecies is distinguishable from *cavernicola cavernicola* only by the smaller eyes and shorter wings. The eye horizontal diameter is 1.50–1.75 times the width of the space between the antennal socket and the anterior eye margin. The eye of *c. cavernicola* is 2.0–2.9 times the width of the eye-antennal space. The wing is 1.2–1.3 times the length of the elytra in *c. aditus* and 1.6 times the elytral length in *c. cavernicola.* Otherwise the description is that of *c. cavernicola* given above, including appendages and male and female genitalia. Measurements of the other structures of this population have not been made to determine if other detectable differences exist.

Etymology. The name *aditus,* Latin, is used as a noun in apposition and refers to the impressive entrance, from which the cave received its name.

Field notes. The 1969 series was taken in the back of the cave in an area with moist bat guano covered with a dense mat of white fungal hyphae. The beetles were abundantly crawling both on the fungal mat and on rocks. The fungal mat was absent in 1971. Human feces were present here and nearby in dryer lower passages but no beetles were found on them. The fauna of the cave is fairly rich and includes a *Nicoletia* thysanuran, collembola, numerous mites, flies, spiders, *Oxidus gracilis* millipedes, histerid and staphylinid beetles, and the carabid beetles *Tachys* and *Rhadine.* The cave is described with a map in Russell and Raines (1967).

Seasonality. Collections have been made only in June and December. Larvae are unknown from either collection.

Distribution and evolution. The subspecies is known only from Cueva de la Boca. This population is 125 air km SSE of the nearest known population at Gruta del Palmito at Bustamante (west of Sabinas Hidalgo). Both caves lie in the limestones exposed in the eastern front of the El Abra Reef Trend.

Both the Gruta del Palmito and Cueva de la Boca *cavernicola* populations exist in similar xeric scrub habitats, and both would seemingly be equally isolated from the Texas populations (the nearest in Val Verde County lying 200 or more air miles to the north) by the low desert between the Mexican and the Texas cave areas. Both Mexican populations were probably in genetic contact with the populations in the rest of the species' range during the Wisconsin glaciation, though Martin and Harrell (1957) find no indication that the arid south Texas region was more favorable for dispersal of mesic fauna in the Wisconsin than now. In the Recent, genetic isolation of the Mexican populations has probably occurred, but only the Cueva de la Boca population has diverged morphologically.

Ptomaphagus gypsum new species
Map 13

Holotype female in MCZ (no. 31960). Type locality: Mexico, Nuevo León, Resumidero de Pablillo (at Pablillo, 55 km SW Linares, 32 km S Galeana). Type data: 4.vi.1966; J. Reddell, D. McKenzie leg.

Diagnosis. The species is characterized by its reduced and unpigmented but distinctly faceted eyes, its wings, which are reduced to 3/4 the length of the elytra, and its habitat in a gypsum cave in the mountains of the Mexican state of Nuevo León. Its eyes are less reduced than in *troglomexicanus* but more than in *cavernicola aditus.* Its antennae and legs are less elongate than in *troglomexicanus* but are more so than in *cavernicola aditus.*

Description. Length 4.0 mm. Width 1.5 mm. Color medium brown. Head finely punctured; eyes reduced, unpigmented, about 30–35 facets indistinctly visible, greatest width on axis at 45° angle from head margin behind eye, maximum length 1.75 times maximum width, space between antennal socket and anterior eye margin equal to maximum length of eye; antennae of medium length, extending to first 1/4 of elytra when laid back, segment II shorter than III and IV, II equal to V and longer than VI, VII longer than broad, VIII transverse, IX and X broader than long. Pronotal sides almost parallel, slightly converging behind, 1.31 times as wide at base as long, hind margin slightly sinuous. Elytra 1.85 times as long as wide at base, external apical angle rounded. Wings reduced to 3/4 length of elytra. Mesosternal carina and notch as in *cavernicola.* Legs slender and elongate. Aedeagus unknown. Spermatheca as in *cavernicola* (Figs. 187–189) but with thinner anterior end when seen in dorsal view.

Etymology. The name is a noun in

apposition referring to the gypsum cave in which the specimen was collected.

Field notes. The type locality cave lies in a dry interior mountain valley. The cave is in Jurassic (?) gypsum with other gypsum caves nearby, and to the north in the vicinity of Galeana. All these could contain the species. A photograph of the area, a description, and a map of the cave is given by Russell and Raines (1967). I searched for the cave in 1969 and was unable to find it with the published information, and I could find no one in Pablillo who knew about a resumidero (a sink at the downstream end of a water course).

Ptomaphagus troglomexicanus Peck
Figures 60, 131, 190; Maps 13, 19

Ptomaphagus (*Adelops*) *troglomexicanus* Peck, 1968: 92. Holotype male in MCZ (no. 31653), seen. Type locality: Mexico, Tamaulipas, Cueva de la Perra, 15 miles NW of Gómez Farías.

Diagnosis. This is the only cave-specialized *Ptomaphagus* known from Mexico. Its tiny unpigmented eyes and very elongate antennae with all segments longer than wide serve to distinguish it.

Description. Length 3.6–4.0 mm. Width 1.7–1.9 mm. Color yellowish to dark brown. Head finely punctured. Eyes reduced to depigmented, faceted spot; head width from antennal base to margin across eye 3 times width of eye. Antennae (Fig. 131) very slender and long, slightly flattened, reaching into first third of elytra when laid back; segment II 2.5 times as long as wide; II and IV subequal, 3.5 times as long as wide; V, VI, and VII sequentially shorter and wider; VII 1.8 times as long as wide; VIII longer than wide; IX 1.3 times longer than wide; X 1.1 times longer than wide. Pronotum widest at base, 1.55 times wider than long; sides slightly divergent behind; hind margin straight. Elytra widest 1/3 from base; 1.55 times as long as wide at base; external apical angles rounded; apex slightly oblique in female, with acute sutural angle. Wings reduced to tiny scale, elytra fused. Mesosternal keel of medium height, notch present. Aedeagus (Fig. 60) long, straight, thin, curved only in basal quarter, tip narrow; in dorsal view, narrowing to broadly sharp tip. Spiculum gastrale long and thin, 2/3 enclosed by genital plates, which are anteriorly elongate and pointed. Spermatheca (Fig. 190) with straight central shaft; twisted at posterior end with 1 1/2 turns; anterior end broad in lateral view, narrow with knob in dorsal view.

Variation. No variation noted.

Field notes. I made collections in Cueva Chica on *Neotoma* (?) dung, on insectivorous bat guano in Cueva Capilla, and carrion bait near the entrance of Cueva de la Mina. The temperature of the first cave is 13°C and that of the third is 15°C. In Cueva Capilla all specimens came from a large mud-flat near the back of the cave. The beetles were feeding on a light sprinkling of guano, in association with troglobitic *Mexisphodrus* and *Paratrechus* carabid beetles. These three caves and others at medium and high elevations in the Sierra de Guatemala of the state of Tamaulipas in Mexico contain a remarkably rich and diverse assemblage of cave-adapted invertebrates. The fauna and the caves are further discussed by Mitchell (1968) and Reddell and Mitchell (1971b). The region, with its cloud forest, is of general biogeographic interest and is discussed by Martin and Harrell (1957), and Martin (1958).

Seasonality. Reproductive seasonality may not occur in this cave species. Adults have been collected only in January, March, and July. Teneral adults are known only from July collections (2 from Cueva de la Mina, and 3 from Cueva Capilla). Larvae are known from a July collection in Cueva Capilla.

Distribution. The species is known only from three caves at an elevation of 5000–7000 feet in the Sierra de Guatemala in Southern Tamaulipas, Mexico. The caves

are six air km distance from each other. I have seen 49 specimens from the following three localities: **MEXICO.** TAMAULIPAS. Cueva Chica de la Perra, 7000′ elev., 11 air km NW Gómez Farías, 6 (SBP); Cueva de la Perra, 7000′ elev., 11 air km NW Gómez Farías, 34 (SBP, MCZ); Cueva de la Mina, 5000′ elev., near Rancho del Cielo, 7 air km NNW Gómez Farías, 8 (SBP).

Distributional comments. The type locality is undoubtedly Cueva Capilla de la Perra. Upon inquiring of inhabitants of the small lumbering town of Charco de la Perra (also called El Porvenir), I was led to two caves. The two caves are less than a quarter of a mile apart. I chose the name Chica to distinguish the small cave from the large cave (which, I was told, was locally known as Cueva Capilla).

It is difficult to reach these caves without a four-wheel drive vehicle. We packed in with burros and supplies to Rancho del Cielo and its caves in one day, where we stayed and worked as guests of Texas Southmost College of Brownsville, Texas, and into La Perra and its caves on a later day. Future workers wishing to collect in the caves and cloud forest of the Sierra de Guatemala should bear these difficulties in mind.

Ptomaphagus oaxaca new species
Figures 64, 65, 135, 191; Map 13

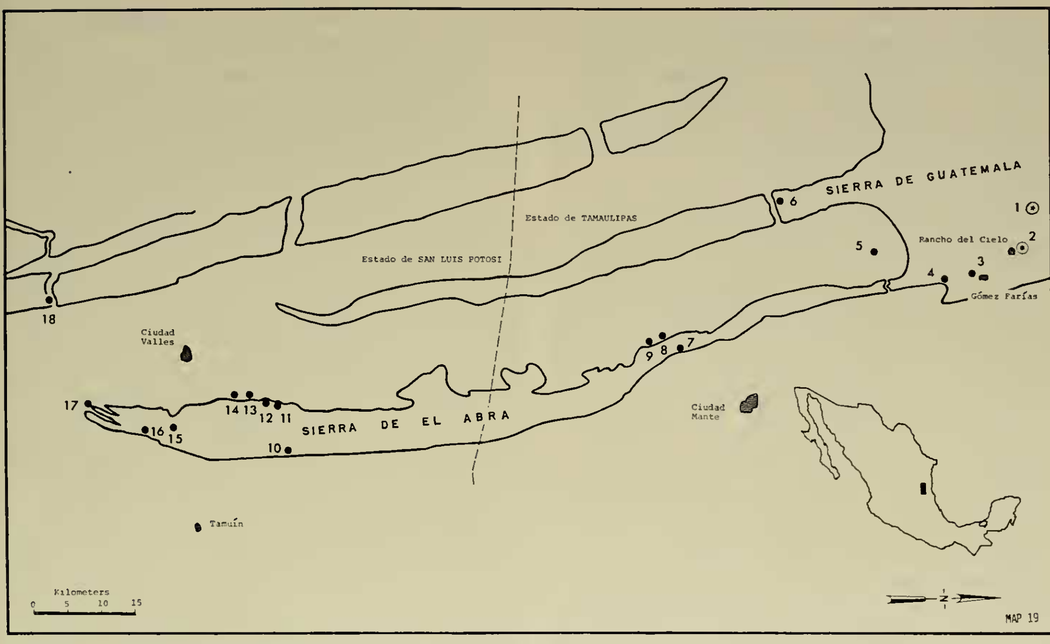
Holotype female and allotype male in MCZ (no. 31965). Type locality: Mexico, Oaxaca, 30 mi. S Valle Nacional on Highway 175. Type data: SE mountain slope, 6800′ elev., cloud forest remnant, 10–13. viii.1970, A. Newton, human dung trap No. 5. Paratypes: all with same date and collector; 5 with above exact data; 5 from 25 mi. S Valle Nacional, W slope, 6350′, rich cloud forest, human dung trap No. 4; 4 from 23 mi. S Valle Nacional, W slope, 5750′, dense cloud forest, human dung trap No. 3; 1 from 35 mi. S Valle Nacional, SE slope, 8000′, low mossy woods, broad-crowned thick-leaved oaks, human dung trap No. 6.

Diagnosis. The species is very similar to *P. cavernicola* and is diagnosed in the same way except for differences in the spermatheca, eyes (larger than in *cavernicola*), and antennae (shorter in *oaxaca*, which has segment II distinctly shorter than III; II, and III are subequal in *cavernicola*).

Description. Length 3.5–3.9 mm. Width 1.8–1.9 mm. Color medium brown, antennal club darker, antennal base lighter. Head finely, densely punctured; eyes large, their horizontal diameter 3.8 times the width of the eye-antennal socket space; antennae long, reaching beyond pronotum when laid back, segment III longer than II, II and IV equal length, V shorter than IV and longer than broad, VI 1.5 times as broad as long; VII 1.15 times wider than long; VIII twice as wide as long. Pronotum widest at base, sides slightly diverging to base, 1.5 times as wide at base as long, hind margin sinuous. Elytra 1.15 times wider than pronotum, widest at middle, 1.65 times as long as wide at base, apex obliquely truncate and sutural angles pointed (Fig. 135) in female. Mesosternal carina low, notch rounded and distinct. Legs long and thin. Spermatheca (Fig. 191) with flattened anterior end and very curved posterior end. Aedeagus long, thin, curved in lateral view (Fig. 64), tip pointed (Fig. 65). Genital segment with long thin spiculum about half enclosed by lateral plates.

Etymology. The name is a noun in apposition and is the name of the mountain range (Sierra Madre de Oaxaca) and of the Mexican state in which the species was collected.

Field notes. The collecting data is given in the type and paratype data. The species was taken in traps along with 26 *Ptomaphagus newtoni*, and 1 female of an unnamed species. Some collecting areas along the road from Valle Nacional to the city of Oaxaca are discussed by Ball and Whitehead (1967).



Map 19. Distribution of *Ptomaphagus troglamexicanus* (circles with stars) and *P. elabra* (solid black spots) in northeastern Mexico. 1 Cueva Capilla de la Perra and Cueva Chica de la Perra, 2 Cueva de la Mina, 3 El Sótano de Gómez Farías, 4 La Cueva del Nacimiento del Rio Frio, 5 El Sótano de las Abejas, 6 La Cueva del Puente, 7 Grutas de Quintero, 8 La Cueva de la Florida, 9 La Cueva de El Pachón, 10 Ventana Jabali (Cave), 11 El Sótano del Tigre, 12 La Cueva de las Sabinos, 13 El Sótano de la Tinaja, 14 El Satanita de Montecillos and el Sótano de Pichijumo, 15 La Cueva de Valdosa, 16 Las Cuevas de Taninul, 17 La Cueva Chica, 18 Cueva de Puente de Dios. Copied in part from privately distributed base map of William H. Russell and Robert W. Mitchell, 1969, and maps in Reddell and Mitchell 1971a, 1971b.

Distribution and evolution. The species is known only from the above collections made in middle and high elevation temperate forests in the Sierra Madre de Oaxaca. This species is probably similar to the ancestor from which *cavernicola* and its derivatives arose.

Ptomaphagus elabra Peck
Figures 62, 63, 128, 196, 211; Maps 13, 19

Ptomaphagus elabra Peck, 1971b: 9. Holotype male and allotype female in MCZ (no. 31895). Type locality: Mexico, Tamaulipas, Cueva de El Pachón, 16 km SSW Ciudad Mante.

Diagnosis. The species is known only from caves at low elevations in the states of Tamaulipas and San Luis Potosí. Its large eyes, short antennae, relatively short and thick aedeagus, and shape of the spermatheca serve to characterize it.

Description. Length 2.6–3.2 mm. Width 1.2–1.5 mm. Color dark brown. Head finely punctured. Eyes normal, their diameter 2.7 times the distance from their anterior margin to antennal base. Antennae (Fig. 128) short, stout, flattened; not reaching pronotal base when laid back; club darker; segments gradually increasing in width from base to apex; segments II–V longer than wide, VI and VIII–X transverse; VII quadrate. Pronotum widest at base; 1.4 times as wide as long; sides gently diverging; hind margin sinuous; pubescence abundant. Elytra elongate; 1.5 times as long as wide as base; widest 1/3 behind base; apex weakly rounded-oblique in female. Wings normal; observed in flight in

Grutas de Quintero. Mesosternum with low keel, notch distinct. Legs medium; mesotibiae bent outward; metatibiae slightly bent inward. Aedeagus (Fig. 62) relatively short and stout, slightly curved; tip fairly blunt in lateral view, in dorsal view (Fig. 63) more blunt, with terminal button. Spiculum gastrale (Fig. 211) long and thin, half enclosed by genital plates, which are not anteriorly elongated. Spermatheca (Fig. 196) with fairly straight and thin central shaft; anterior end with shaft bent posteriorly, then ventrally and curving to anterior flattened end; posterior end somewhat laterally flattened, thin in dorsal view.

Variation. Variation is noticed in slide mounts of the aedeagus in which the tip is rotated to appear more broad.

Etymology. The name *elabra* is used as a noun in apposition. It refers to the Sierra de El Abra, which contains most of the caves from which the species is known.

Field notes. The species was found abundantly in dryish insectivorous bat guano in Cueva del Nacimiento del Rio Frio, and in Cueva Ventana Jabili. In Grutas de Quintero 134 were found in the felt lining of a severed toe of a boot. In Cueva de El Pachón 119 were taken from pools of liquid vampire guano. The beetles walked freely and rapidly on the liquid guano, showing no tendency to get stuck in the viscous mess. The beetles show no unusual tarsal features that would account for this ability. No other species has been observed on the surface of liquid vampire guano.

The cave temperatures are 24–25°C. The elevations are all under 800 m.

Seasonality. Reproduction probably occurs throughout the year. Adults have been collected in every month except May, August, and October. Teneral adults are known from Cueva de El Pachón (8 out of 119), Grutas de Quintero (27 out of 138), Cueva del Nacimiento del Rio Frio (9 out of 31), and Ventana Jabili (2 out of 24). All were collected in late June and early July. Larvae have been found in two caves in June and July.

Distribution. The species is known only from lowland caves in and near the Sierra de El Abra, a north-south trending low range in the Mexican states of Tamaulipas and San Luis Potosí. I have seen 475 specimens from the following 19 localities:

MEXICO. SAN LUIS POTOSÍ. Cueva Chica (2 1/2 km NE El Pujal), 1 (SBP); Cueva de Puente de Dios (30 km SSW Valles), 3 (SBP); Cueva de los Sabinos (12 1/2 km NE Valles), 3 (SBP); Cueva de Taninul No. 1 (13 1/2 km SE Valles), 1 (SBP); Cueva de Valdosa (10 1/2 km SE Valles), 9 (SBP); Sótano de Manuel (3 km NE El Pujal), 1 (SBP); Sótano de Montecillos (10 km NE Cd. Valles), 1 (SBP); Sótano de Pichijumo (8 km NE Valles), 1 (SBP); Sótano del Tigre (14 km NE Valles), 9 (SBP); Sótano de la Tinaja (10 1/2 km NE Valles), 9 (SBP); Ventana Jabili (20 km E Valles), 27 (SBP). TAMAULIPAS. Bee Cave (19 km NW Limon), 13 (SBP); Cueva de la Florida (8 1/2 km NE Antiguo Morelos), 19 (SBP); Cueva del Nacimiento del Rio Frio (7 km S Gómez Farías), 31 (SBP); Cueva de El Pachón (7 1/2 km NE Antiguo Morelos, type locality), 119 (SBP); Cueva de los Vampiros (20 km NW Limon), 23 (SBP); Grutas de El Puente (9 km SE Ocampo), 6 (SBP); Grutas de Quintero (Quintero, 13 km SW Cd. Mante), 178 (SBP); Sótano de Gómez Farías (2 1/2 km SW Gómez Farías), 2 (SBP); Sótano de Santa Elena (9 km SE Antiguo Morelos), 19 on vampire guano (SBP).

Distributional comments. Though the species is now known only from lowland caves, I do not think it is restricted to them. Though we were unable to collect it in epigean habitats, it should be expected in moist and forested situations in the Sierra de El Abra or other lowland or midmontane localities.

It is conjectural as to whether the species is presently dispersing overland between caves of the Sierra de El Abra. I have

seen individuals in flight, so this dispersal method is available to them.

The general area of the Sierra de El Abra is xeric. The vegetation is mostly a lowland tropical thorn forest, with protected ravines and streamsides possessing a tropical deciduous forest. Under certain climatic conditions, such as damp nights, dispersal may occur between caves and favorable noncave situations.

An alternative but less likely explanation is that the species is now completely restricted to the caves because of moisture or other requirements. The restriction may have occurred with changing climatic conditions of the Pleistocene, most likely following the Wisconsin glacial retreat.

A discussion of the El Abra caves and their fauna, with emphasis on cave evolution, is that of Mitchell (1969). A list of the total El Abra cave fauna is given by Reddell and Mitchell (1971a).

Ptomaphagus jamesi new species
Figures 70, 71, 197; Map 13

Holotype female and allotype male in MCZ (no. 31963). Type locality: Mexico; Oaxaca, 5 km W San Cristobal de las Casas. Type data: 16.viii–2.ix.1969, S. & J. Peck, 8000′ elev., pine-oak forest, carrion bait trap. Paratypes: 1 female and 1 male same as above, 6 males as above but 13–16. viii.1969, carrion trap.

Diagnosis. The species is characterized by the spermatheca with a thin anterior profile, broadly pointed (ogival) aedeagus tip, large finely faceted eyes, and rounded nonpruinose sutural angles of the female elytra.

Description. Length 2.9–3.4 mm. Width 1.4–1.6 mm. Color medium-dark brown, head and antennal club darker. Head with large, finely faceted eyes, their horizontal diameter 2.3–2.9 times the width of the eye-antennal socket space; antennae medium length, reaching just beyond pronotal base, segment III 6/7 as long as II, IV 3/4 as long as III, V as long as IV, and 8/9 as wide at apex as broad, VI 7/9 as long as wide, VII longer than wide, VIII–X transverse, VIII twice as wide as long. Pronotum with sides slightly diverging at base, 1.5 times as wide at base as long, hind margin sinuous. Elytra widest 1/3 from base, 1.5 times as long as wide at base, sutural angles and apex rounded in both sexes, no pruinose areas on female elytral tips. Mesosternal carina low, notch normal. Wings present. Legs robust. Aedeagus (Fig. 70) curved, thin, tip (Fig. 71) broadly pointed. Spermatheca (Fig. 197) with narrow anterior part, twisted posterior end. Genital segment as in *P. altus*.

Etymology. The species is named for my brother, James Peck, in recognition of his assistance to me in field work in the summers of 1965 and 1969.

Field notes. The above 10 specimens were taken in a temperate forest along with 69 specimens of *P. altus*. The forest is described with this later species.

Distribution and evolution. The species should probably be expected in other high elevation pine-oak forests of southern Mexico and perhaps Guatemala. Because of its larger eyes it may not be as old or as obligate a montane inhabitant as is *P. altus* to which it is generally similar.

Ptomaphagus altus new species
Figures 68, 69, 129, 137, 194; Map 13

Holotype female and allotype male in MCZ (no. 31962). Type locality: Mexico; Chiapas, 5 km W San Cristobal de las Casas. Type data: 16.viii–2.ix.1969, S. & J. Peck, 8000′ elev., pine-oak forest, carrion bait traps. Paratypes: 29 males and 14 females with same data; 7 males and 9 females from same locality but 13–16.viii. 1969 in carrion-baited traps.

Diagnosis. The species is recognized by the combination of characters of the aedeagus, spermatheca, rounded female sutural elytral angles, and somewhat reduced and more coarsely faceted eyes.

Description. Length 3.0–3.4 mm. Width

1.4–1.5 mm. Color dark brown. Head sparsely punctured; eyes reduced and with coarse facets, their horizontal diameter 1.9–2.0 times the width of the eye-antennal space; antennae short, not reaching base of pronotum when laid back, segments (Fig. 129) II and III equal, IV–VI successively shorter and broader, VII quadrate. Pronotum widest 1/3 before base, sides slightly converging to base, 1.2 times as wide at base as long; hind margins sinuous. Elytra wider than pronotum, 1.45 times longer than wide at base; hind margin, and sutural angles rounded in both sexes (Fig. 137); elytral tips with pruinose patch along suture in females. Wings present. Mesosternal carina medium, notch large and rounded. Legs average length. Aedeagus thin and curved with button at tip (Fig. 68), tip in dorsal view pointed (Fig. 69). Genital segment with spiculum mostly enclosed by lateral plates. Spermatheca (Fig. 194) with broad anterior margin.

Etymology. The name (Latin, *altus*, high) is used as a noun in apposition and refers to the high-elevation forests in which the species was collected.

Field notes. The type series was captured in traps at the edge of a wooded ravine, at the oak forest at the sharp bend in the main highway west of San Cristobal. The ravine vegetation was of temperate aspect and included *Quercus, Pinus, Arbutus, Rubus, Crategus, Carpinus,* and *Alnus.* Ten specimens of *P. jamesi* were taken at the same locality.

Variation and distribution. Another specimen that is assigned to this species is a female bearing the following data: Mexico: Michoacan, 40 km E Morelia at Mil Cumbres, 8–10.ix.1969, S. & J. Peck, 9000′ elev., pine-oak forest, carrion-dung traps. It agrees with the Chiapas specimens in most characters. However, its elytra are less rounded and its mesosternal notch much smaller and narrower. This record suggests that the species or other reduced-eyed ones close to it may be distributed in other high elevation localities with pine-oak forests in the southern and western mountains of Mexico.

Ptomaphagus newtoni new species
Figures 66, 67, 136, 195; Map 13

Holotype female and allotype male in MCZ (no. 31964). Type locality: Mexico; Oaxaca, 25 mi. S Valle Nacional on Highway 175. Type data: W slope of mountain, 6350′ elev., rich cloud forest, 10–12.viii. 1970, A. Newton, human dung trap No. 4. Paratypes: 5 females and 7 males with above data; 2 males with above data but from 23 mi. S Valle Nacional, W slope, 5750′, dense cloud forest, human dung trap No. 3; 4 males and 5 females as above but from 30 mi. S Valle Nacional, SE slope, 6800′, cloud forest remnant, human dung trap No. 5.

Diagnosis. The species is characterized by the spermatheca, pointed aedeagus tip, rounded female elytral sutural angles, large eyes, and short antennae.

Description. Length 2.9–3.5 mm. Width 1.4–1.6 mm. Color medium brown, head and antennal club darker. Head with eyes large, their horizontal diameter 3.5 times the width of the eye-antennal socket space; antennae short, reaching only base of pronotum when laid back, segment III longer than II, IV 3/4 length of II, IV and V equal length, V 9/11 as long as broad at apex, VI 2/3 length of V, VII broader than long, VIII 3.5 times as wide as long, IX and X broader than long. Pronotum widest at base, sides parallel behind, 1.45 times as wide at base as long, hind margin sinuous. Elytra wider than pronotum, widest 1/3 from base, 1.6 times as long as wide at base, sutural angles and apex rounded in both sexes (Fig. 136), not pruinose along suture at apex in females. Wings present, normal. Mesosternal carina medium, notch medium. Legs short, robust. Aedeagus (Fig. 66) pointed and curved in lateral view, tip pointed in dorsal view (Fig. 67). Genital plates half enclosing spiculum. Spermatheca (Fig. 195) with broad, shal-

lowly grooved anterior end, straight middle piece, and moderately twisted posterior end.

Etymology. The species is named for Al Newton in recognition of his help in the field and his making available to me his collections and data.

Field notes. The species was taken at the same montane forest trap sites as *P. oaxaca,* and one female of an unnamed species.

Distribution. The species is known only from the above collections in the middle- and high-elevation temperate forests of the Sierra Madre de Oaxaca.

Ptomaphagus leo new species
Figures 61, 130, 193, 210; Map 13

Holotype male and allotype female in MCZ (no. 31894). Type locality: Mexico; Nuevo León, Chipinque Mesa (5400′ elev., at Monterrey). Type data: 21–25.vi.1969, S. and J. Peck leg., human dung traps in forest. Paratypes: 28 with same data.

Diagnosis. The species is characterized by the small, thin aedeagus; very twisted spermatheca; and especially by the genital plates, which are projected anteriorly along the spiculum gastrale but enclose only half of the long and thin spiculum.

Description. Length 2.5–3.2 mm. Width 1.2–1.4 mm. Color dark brown. Head with numerous punctures forming faint striae; eyes normal, large; 5 times as wide horizontally as space between antennal base and anterior eye margin. Antennae (Fig. 130) normal, short, flattened; segment II longer than III; IV and V subquadrate; VI–X transverse. Pronotum widest at base; 1.4 times as wide at base as long; sides slightly divergent; hind margin sinuous. Elytra widest 1/3 behind base; 1.5 times as long as wide at base; apex oblique in females, sutural angle slightly rounded. Wings normal. Mesosternal carina low, notch present. Legs normal; mesotibiae bent outward; metatibiae slightly bent inward. Aedeagus (Fig. 61) small, thin, curved; tip blunt; in dorsal view tip with sides evenly converging to narrowly truncate point. Spiculum gastrale (Fig. 210) long and thin, half enclosed by genital plates which are elongated anteriorly. Spermatheca (Fig. 193) thin, twisted; posterior end turning once then turning back and over to end; anterior end thin in dorsal view; broad in lateral view.

Variation. No variation noted.

Etymology. Latin, *leo,* lion, a noun in apposition referring to the Mexican State of Nuevo León, from which the species is known.

Field notes. The species has been taken only at two localities. At Chipinque Mesa ten were taken in malt traps (by H. Howden), 30 in three human dung, and 5 in two canned dog food baited traps, 7 in a Berlese extraction of 176 liters (166 pounds) of forest soil and leaf litter, and one in a small cave. Three were taken near guano in both entrance and dark zones of Cueva de Chorros de Agua.

Seasonality. Only dark adults are known from collections made in June and August. Larvae are not known.

Distribution. Presently it is known only from two localities separated by 80 air km in the state of Nuevo León. I have seen 56 specimens from the following two localities: **MEXICO.** NUEVO LEÓN. Chipinque Mesa, 5400′ elev. (at south edge of Monterrey), 53 (CNCI, MCZ, SBP); Cueva de Chorros de Agua (13 mi. W Montemorelos), 3 (SBP).

Distributional comments. Chipinque Mesa is the northernmost locality in the Mexican Sierra Madre Oriental containing mesic forest. We noticed several plants common to the southeastern United States (redbud, *Cercis;* poison oak, *Rhus;* hickory, *Carya;* and catbrier, *Smilax*) that have distributional disjunctions, being absent from xeric south Texas and the adjacent lowlands of Tamaulipas and Nuevo León. In insect distributions, Chipinque Mesa is the northern locality of mesic Mexican species (Howden, 1966).

Ptomaphagus spelaeus (Bilimek)
Figures 72, 73, 138, 192; Map 13

Choleva spelaea Bilimek, 1867: 902. Type in Museum Vienna, not seen. Type locality: Mexico, Guerrero, Cueva de Cacahuamilpa.
Choleva cacahuamilpensis Herrera, 1891: 218. Type repository unknown, not seen. Type locality: Mexico, Guerrero, Cueva de Cacahuamilpa. Synonymized *in* Peck, 1971b: 11.
Dissochaetus spelaea, Jeannel, 1922: 41.
Ptomaphagus (*Adelops*) *spelaeus,* Jeannel, 1936: 93; 1949: 98. Peck, 1971b: 11.

Note on deposition of type. Although Jeannel has stated that the type of the species is in Vienna, Dr. F. Janczyk of the Zoologische Abteilung, Naturhistorisches Museum Wien, has searched the collection and cannot find it (in litt.).

Diagnosis. The species is characterized by the shape of the spermatheca, the aedeagus tip which is bluntly pointed in dorsal view, and with a ventral button in lateral view, the rounded female elytral tips, medium antennae, large eyes, and cave habitat in west-central Mexico.

Description. Length 2.6–3.2 mm. Width 1.2–1.5 mm. Color dark brown. Head with eyes large and prominent, their horizontal diameter 2.7 times width of eye margin-antennal socket space. Antennae slightly lighter in color at base, medium length, scarcely surpassing pronotal hind margin when laid back, segment II 5/12 as wide as long, III 1/2 as wide as long, IV and V slightly longer than wide, VI and VII wider than long, VIII 5/12 as wide as long. Pronotum with sides slightly converging behind, widest at middle, 1.8 times as wide at base as long, hind margin sinuous. Elytra 1.5 times as long as wide at base, sutural angles and hind margin rounded in males and females (Fig. 138), pruinose at tip along suture in females. Fully winged. Legs medium, metatibiae bent inward. Mesosternal carina medium, notch distinct. Aedeagus thin, curved, with terminal ventral button in lateral view (Fig. 72), tip bluntly rounded in dorsal view (Fig. 73). Genital plate half enclosing spiculum. Spermatheca as in Figure 192.

Field notes. From the type locality, Cueva de Cacahuamilpa, Bilimek reported the beetles as running rapidly over cave flowstone. Herrera found one near "Agua bendita." I visited this cave in 1969 but could not collect. It has been commercialized and is heavily visited by tourists. The commercialization may have altered conditions so that the beetles no longer live there. James Reddell (in litt.) found none in a collecting visit to the cave in 1965. In Gruta de Acuitlapan 18 were collected in the first gallery and 12 in the second gallery.

Distribution. I have examined the following material: **MEXICO.** GUERRERO. Gruta de Acuitlapan (12 km E Taxco), 1 (9.iv.1968, W. Calvert, SBP), 30 (2.vi.1963, C. Bolivar, J. Hendrichs, J. Urquijo, SBP, JHSC, ENCB). Resumidero del Rio San Geronimo, near Michapa, 1 (18.x.1942, C. Bolivar, D. Pelaez, ENCB).

Distributional comments. Though I have not seen material from the type locality for comparison, there is no doubt that the above collections represent the species. The type cave, and the two listed above, are all near one another in the same karst region. These caves possess the same general fauna. Several other caves exist in the vicinity (Fish, 1966) and probably contain the species. As evidenced by the distributional data, there is no doubt that Herrera's species is a synonym.

The region possesses rugged topography with a scrubby vegetation. It is xeric in appearance. That the beetle also exists in noncave habitats in the region is conjectural. It does not possess a cave-adapted morphology. Both surface and cave collecting are needed in this section of Mexico.

Cavernicola Group Incertae Sedis

The following material represents collections of *Ptomaphagus* in the *cavernicola* group from Mexico and Guatemala. I tentatively judge them to be new species but believe my material is inadequate to serve as the basis for distinctive and com-

plete descriptions and characterizations of new species. I am taking this conservative position to prevent the possibilities of future taxonomic problems arising from names based on inadequate material. I encourage future workers to be as cautious when dealing with this complex fauna in Mexico and Central America, and to try to work seriously only with good population samples of the difficult species in this group. I am providing the following list to make available the seasonal, ecological, and distributional data and to encourage further collecting efforts in these areas.

Species 1

Mexico: Oaxaca; 23 mi. S Valle Nacional on Highway 175, 5750′ elev., dense cloud forest, 9–12.viii.1970, A. Newton, human dung trap No. 3, 1 female; taken with *P. oaxaca* and *P. newtoni*.

Species 2

Guatemala: Alta Verapaz; Patal, 5 km S Tactic, 24–27.viii.1969, S. & J. Peck, 4500′ elev., cloud forest, 1 in trap; taken with following species.

Species 3

Mexico: Chiapas; Lagunas de Montebello, near Comitan, 14–17.viii.1969, S. & J. Peck, 4500′ elev., tropical montane forest, 4 in trap. Guatemala: Alta Verapaz; Patal, 5 km S Tactic, 24–27.viii.1969, S. & J. Peck, 4500′ elev., cloud forest, 1 in trap, 1 on dead millipede.

Species 4

Mexico: Veracruz; Cordoba, 4–6.viii. 1969, S. & J. Peck, tropical evergreen forest, 1 in trap. Fortin, 5–8.viii.1969, S. & J. Peck, tropical evergreen forest, canyon Rio Metlac, 2 in trap. Huatusco (1.2 mi. S), 1344 m elev., 5–8.viii.1969, S. & J. Peck, cloud forest, 5 in trap. Hidalgo; 10 mi. SW Jacala, 1–3.viii.1960, H. Howden, 1 in malt trap, CNCI.

Species 5

Mexico: Querétaro; 25 mi. E Landa de Matamoros, 5000′ elev., 14–17.vii.1969, S. & J. Peck, *Liquidambar* forest, 1 in trap. Pueblo; Nuevo Necaxa, 25–28.vii.1969, S. & J. Peck, 1200 m, sycamore forest, 1 in malt trap.

Species 6

Mexico: Tamaulipas; Gómez Farías, Rancho del Cielo, 5000′, Cueva de la Mina, 1.vii.1969, S. & J. Peck, 2 in debris at cave entrance. 3700′, 1–4.vii.1969, S. & J. Peck, cloud forest, 2 in trap.

Species 7

Mexico: Oaxaca; Huatla, 1700 m, 9.iv. 1969, forest litter, K. Kowalski leg., 7 (PISZ).

Incertae Sedis

The following three species are known only from male material and cannot be reasonably placed in species groups based upon female characters. Two of the species are new, but I believe they are distinct enough that no future problems will be encountered in recognizing them.

Ptomaphagus championi Jeannel
Figure 133; Map 13

Ptomaphagus consobrinus, Matthews, 1888: 100.
Ptomaphagus (*Adelops*) *championi* Jeannel 1936: 93. Type male in British Museum (Natural History), seen. Type locality: Guatemala, in mountains near Santa Cruz del Quiché. Jeannel, 1949: 98 (systematics).

Diagnosis. Known only from the type, from Guatemala. Its eyes are reduced, the antennal segments II and III are twice as long as wide, and the pronotum is widest at the base.

Description. The description is based

upon those of Matthews (1888) and Jeannel (1936) as well as my inspection of the type (which exists in a fragmented condition, missing the prothorax, most of the head, and the abdomen). Length 2.50 mm. Width at elytral base 1.2 mm. Color medium brown (castaneous); clothed with long sparse pubesence. Head with eyes rather small, not prominent; antennae (Fig. 133) moderate, first two segments lighter color, segments II and III twice as long as wide, IV and V a little longer than wide, VI and VII only slightly wider than long, VIII 3 times as wide as long, IX and X transverse. Pronotum widest at base, sides slightly curved, hind angles acute, striae distinct. Elytra rather attenuated posteriorly, scarcely broader but twice longer than the head and thorax, widest at base; sides scarcely rounded; external apical angles rounded; apex obtuse; striae oblique. Winged. Legs moderately elongate. Mesosternal carina prominent, notch large, quadrangular. Genitalia unknown.

Notes on the type. The type specimen does not exist in sufficiently good condition to clearly characterize the species. The prothorax is missing, but one prothoracic leg and all other legs are present. The head is partially missing so that I cannot measure the eye size, but both antennae are present and glued to the mounting card. A bit of wing is visible beneath the elytra but the elytra were not relaxed and lifted to accurately observe the wing condition. The abdomen is missing, so the genitalia are unavailable.

Distribution and ecology. The type was taken near Santa Cruz del Quiché (Dept. of El Quiché) in the Quiché mountains (a western part of the Sierra de Chuacús) at an elevation of from 7–9000 feet. No other data is available. The Central America (Coban quadrangle) map 1:250,000 shows these mountains with a summit at 2607 m with a road (from Santa Cruz to Santa Rosa Chujuyub) going to 2558 meters. This is the logical place to look for forests in the future in an attempt to secure the species. It may exist, however, at other localities, at lower elevations. In my 1969 collecting in Guatemala I was not able to collect in the Chuacús Mountains. I do not believe any of the three specimens I collected in Guatemalan forests in the Dept. of Alta Verapaz represent this species.

Ptomaphagus meximontanus new species
Figures 75, 76; Map 13

Holotype male in MCZ (no. 31959). Type locality: Mexico; Querétaro, 9 mi. NW Pinal de Amoles, 4 mi. NE Rio Blanco (17 mi. W Jalpan). Type data: 9.vii.1967; J. Reddell, J. Fish, B. Russell; 9000′ elev., broad forested draw. Paratype (SBP) data: one male; Mexico; Querétaro, Tejamanil (3.0 mi. SW of Pinal de Amoles); 9.viii.1966, J. Reddell, J. Fish, D. McKenzie, 3000 m elev., under rock.

Diagnosis. The species is characterized by its winglessness, its eyes whose width is equal to the width of the space between their inner margin and the antennal insertion, and its habitat in high montane Mexican forests.

Description. Length 2.7 mm. Width 1.2 mm. Form elongate oval. Color dark brown. Head shining, with a few punctures; eyes reduced, pigmented, with about 45 facets, their horizontal width less than vertical width, horizontal diameter equal to the space between their anterior margin and the antennal socket. Antennae normal, medium length, flattened; segments II and III equal; IV–VI sequentially shorter; VI transverse. Pronotum widest at middle, 1.47 times as wide at base as long, narrowing slightly at base; striae distinct. Elytra slightly wider 1/4 behind base; 1.25 times as long as wide; external apical angles rounded; apex obliquely truncate; sutural angle rounded in males. Wings absent. Mesosternal carina low, notch small. Legs normal; mesotibiae bent outward, metatibiae slightly bent inward. Aedeagus (Fig. 75) slightly curved, narrowing slightly to

apex, tip thin; in dorsal view (Fig. 76) tip wide. Spiculum gastrale normal, slightly over half enclosed by genital plates, which have slight concavity on edges forming border of genital aperture. Spermatheca unknown.

Variation. No variation noted.

Etymology. The name is a noun in apposition referring to the known habitat of the species, high montane forests in the Mexican state of Querétaro.

Field notes. The known habitat data is given for the specimens. In 1969 and 1971 I briefly and unsuccessfully searched for the species at Tejamanil. The forests are of pine and oak on limestone.

Distribution and evolution. The species is known only from two specimens taken in the same high forested mountains at Pinal de Amoles. The reduced eyes and wingless condition suggest that the species has limited dispersal capabilities and may be limited to these particular mountains in western Querétaro.

The male genital structures and the beetles' size suggest membership in the *consobrinus* species-group. With no known females this can not now be certain. It will be of evolutionary interest to learn if this montane edaphophile is a relict species of the *hirtus* or *consobrinus* groups, which do not now inhabit eastern Mexico. Its size and shape, the male genital structures, and the small eye suggest relationship to *californicus*. The eye of *californicus* is also smaller than normal in the genus, but is still larger and more distinctly faceted than in *meximontanus*.

Ptomaphagus talamanca new species
Figures 74, 132; Map 13

Holotype male in CNHM. Type locality: Panama, Chiriquí Province, Finca Lerida, near Boquete. Type data: trail below "Casita Alta," alt. 68–6900 ft., 18 March 1959. G. A. Solem leg.

Diagnosis. This is the only *Ptomaphagus* known from south of Guatemala except for the *Ptomaphagus* (*Tupania*) of Brazil. It is distinguished by its elongate antennae, with only segment VIII being wider than long, and the eye whose horizontal diameter equals the space between the eye and the antennal insertion. The antennal segments are broader than in the cave-inhabiting *giaquintoi* of Guatemala.

Description. Based solely on the unique holotype. Length 3.6 mm. Width 1.9 mm. Form elongate oval. Color dark brown. Head finely sparsely punctured. Eyes reduced, faceted, pigmented; head width across eye from margin to antennal insertion 2.0 times eye width. Antennae (Fig. 132) elongate, flattened and stout; reaching into first quarter of elytra when laid back; all segments but VIII longer than broad; II, III, and IV twice as long as broad; III longer than II and IV; VII elongate conical, 3/4 as wide as long; VIII 1.25 times as wide as long; IX and X 1.1 times as long as wide. Pronotum 1.2 mm long, 1.85 mm wide; widest 1/3 before base; sides arcing weakly behind to acute hind angles; hind margin straight; striae distinct. Elytra narrower than pronotum, widest 1/3 behind base; 2.4 mm long; 1.75 mm wide at base; external apical angle rounded; apex truncate; sutural angle slightly rounded; striae strong, weakly oblique to suture. Wings absent, elytra fused. Mesosternal carina low, notch distinct. Legs with only mesotibiae curved. Aedeagus (Fig. 74) long, slightly curved, blunt at tip; in dorsal view tip very blunt, rounded. Spiculum gastrale long and thin, half enclosed by genital plates, which are somewhat produced anteriorly. Spermatheca unknown.

Etymology. The name *talamanca* is used as a noun in apposition. It refers to the mountain range of western Panama and southeastern Costa Rica in which the beetle was collected.

Distribution. The species is known only from the type locality. It is probably a forest litter inhabitant of high and medium elevations in the Talamanca mountain range.

Distributional comments. Although the species is now known from only one specimen, it seems useful to describe it at this time. The collection serves to partially fill the distributional gap existing between the *Ptomaphagus* of Guatemala and those of northern and southern Brazil.

PHYLOGENY AND ZOOGEOGRAPHY

As is true in most other groups of terrestrial invertebrates, consideration of the phylogeny and distributional history of the Ptomaphagini must be based upon living species because of a very limited or nonexistent fossil record. I know of only one reported fossil for this group of beetles, *Ptomaphagus germari* Schlechtendal (1888) from the Baltic Amber.

For purposes of historical perspective, the ideas of Jeannel on the evolution and distribution of the tribes will be presented first. I will then present the contrasting evolutionary scheme of Szymczakowski, with which I agree, and will add new details and interpretations on the history of the genera. I will then present my own ideas of the evolutionary and distributional history of the New World species of *Ptomaphagus*.

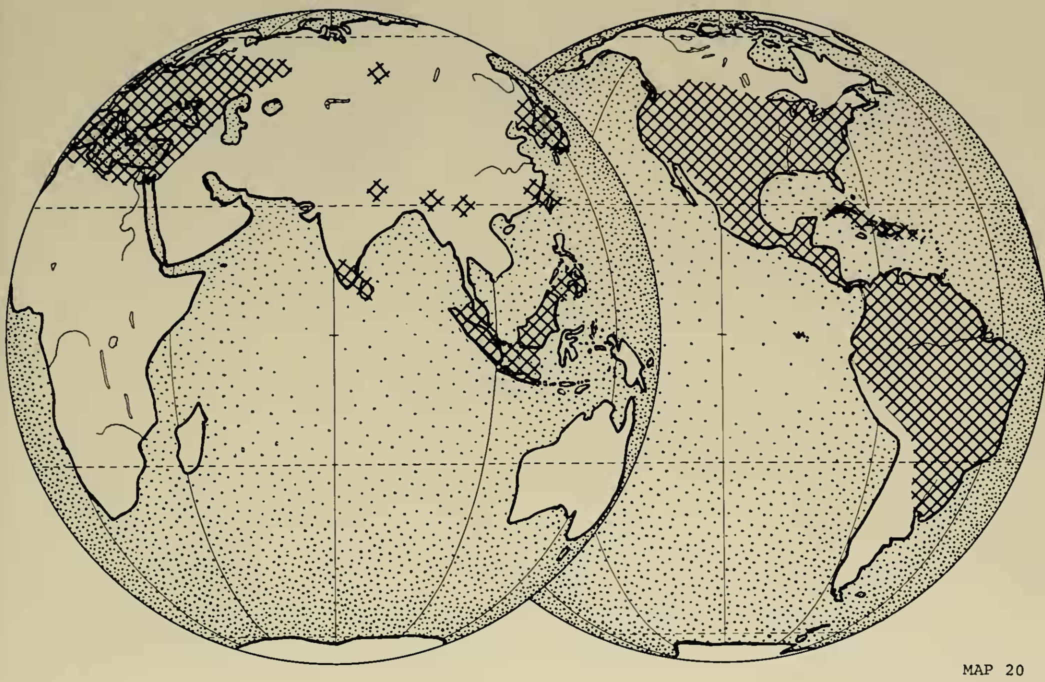
The ideas of Jeannel trace (with modifications) through quite a series of papers (1922: 35; 1936; 1942: 28; 1961: 55; 1964). Jeannel's line of reasoning sprang from a belief in the truth of three major initial assumptions. 1) The origin of the tribe was in tropical America, because this is the region of greatest present diversity. 2) He utilized the Wegenerian concepts of continental drift. I am not here arguing for or against drift, but I believe simply that it is not necessary for understanding the history of the Ptomaphagini. 3) The last assumption, with which I agree, has to do with the evolutionary modification of the morphology of the male aedeagus of members of the tribe. It is as follows: In the tribe Ptomaphagini there has been selection for a migration of the position of the apical genital orifice, the orifice through which the internal sac is everted at the tip of the aedeagus. The tendency is for the orifice to shift from the ventral and median (primitive) position to the dorsal surface of the aedeagus. Jeannel gives no explanation for the selective or adaptive advantage of a dorsal genital orifice, and I can offer none. When this migration has occurred, it has done so by cutting across either the right side or the left side of the aedeagus.

The rest of the story, as interpreted by Jeannel, is found in his most recent papers (1961: 55, 1964), and the following is a summary, in which I use my supra-generic categories.

The primitive ancestors of the Ptomaphagini arose on the Gondwana land mass in the Jurassic. By the Cretaceous, these ancestral populations were displaced to two extremities of Gondwana by "centrifugal segregation." One displaced population would come to occupy those areas that are today the Indo-Malayan region. These species possessed an aedeagus having a tendency to shift the apical orifice so that it cut across the right side of the organ (dextrogyral). This dextrogyral group was to become the subtribe Ptomaphaginina and the genus *Ptomaphaginus*.

On the other side of the ancient Jurassic continent other lines differentiated in the Brazilian massif, which by the Cretaceous was thought to stretch to the north through the lands of Archiguyane and the lands of the Caribbean. In the Cretaceous stocks in South America, the migration of the orifice was effected by cutting across the left side of the aedeagus (sinistrogyral). These sinistrogyral stocks established the subtribe Ptomaphagina and were predecessors of the genus *Adelopsis*.

Jeannel continues by thinking that throughout the Cretaceous, the ancestors of the genus *Adelopsis* experienced many attempts at a successful sinistrogyral migration of the copulatory orifice. In some, the orifice migration occurred near the apex, and often resulted in hyperplastic



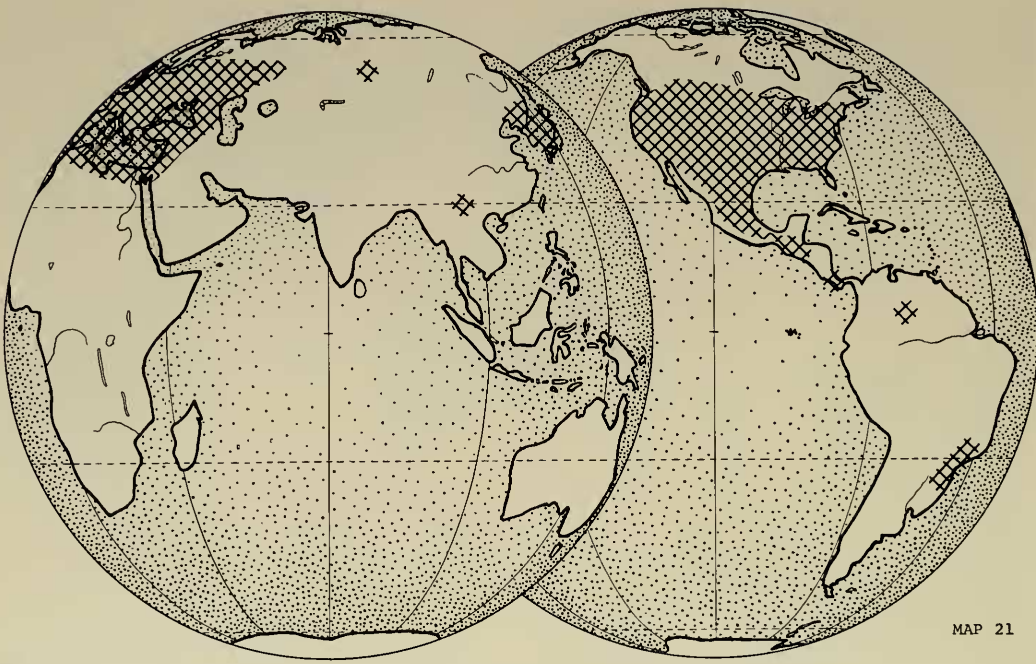
Map 20. Present distribution of the tribe Ptomaphagini.

and monstrous morphologies. In others, the orifice migration passed far from the apex. From these there evolved a new type of sinistrogyral aedeagus which was "successful and harmonious." This later successful stock migrated northward during the Eocene into North America, and from there eventually into all of the Palaearctic region via Europe. The ancestors that successfully distributed themselves throughout the Holarctic region were to become the genus *Ptomaphagus*.

The myrmecophilous *Synaulus* of North Africa are descendants from the first *Ptomaphagus* immigrants to Europe (in the Eocene?, Jeannel, 1922). This earlier paper is also interesting for comparing Jeannel's earliest and latest ideas on dispersal routes. In 1922 he believed that the European *Ptomaphagus* were directly descendant from an ancestral migration of *Adelopsis* from South America via a trans-Atlantic land bridge. The European *Ptomaphagus* then recrossed the Atlantic into North America, giving rise to the subgenus *Adelops* and the cave-inhabiting species.

With Jeannel's earlier concept of continental drift, he believed it was not unreasonable that two trans-Atlantic crossings were more probable than one crossing of the water gap, which is wider in the drift concepts, between North and South America.

In support of this, there are now plausible biogeographic arguments that can be developed to support the hypothesis that eastern North America and Europe were joined early in Tertiary time by a land connection extending across the North Atlantic through Greenland, Iceland, the Faeroes, and the British Isles (Löve and Löve, 1963; Kurten, 1966). The plausibility of these arguments are greatly strengthened by the recent application of paleomagnetic data to demonstrate that the ocean floor



Map 21. Present distribution of the genus *Ptomaphagus.*

has apparently been actively spreading, widening the gap between the continents, for at least several million years (Vine, 1966). However, even though the above considerations allow the possibility of trans-Atlantic connections, faunal studies (Lindroth, 1957) have concluded that the land connections can not have operated with any impact on the fauna of North America and Europe after the early Tertiary.

The zoogeography of the higher groups of the Catopinae as viewed by Szymczakowski (1964) is more reasonable than that of Jeannel. The movements of the beetles are related to geological and paleoclimatic events that have a demonstrable basis in fact. Two later papers (Szymczakowski, 1968; and Peck, 1970a) add more data, which, when considered with the data in this paper, lead me to propose the following history of the Ptomaphagini and its included groups. I think this history accounts for the present facts of distribution of the tribe (Map 20) and the genus (Map 21) when considered in conjunction with the phylogeny proposed in Figure 212.

History of Ptomaphagini. The following speculations on generic divergence are presented in Figure 212. I use the clues and their interpretations suggested by Darlington (1957: 31) as an operational basis for my model.

The tribe originated in the Americas in subtropical or mildly seasonal warm temperate forests. This climatic region presently is the area with the highest numbers and diversity of genera and species. This broad American region presently contains four genera in the two subtribes, compared with two genera in one tribe in the Oriental Region and two genera in one tribe in the Palearctic Region. The nearest related tribe is the Eucatopini, containing only one genus, in which all species are Neotropical. The greatest present generic and specific diversity in

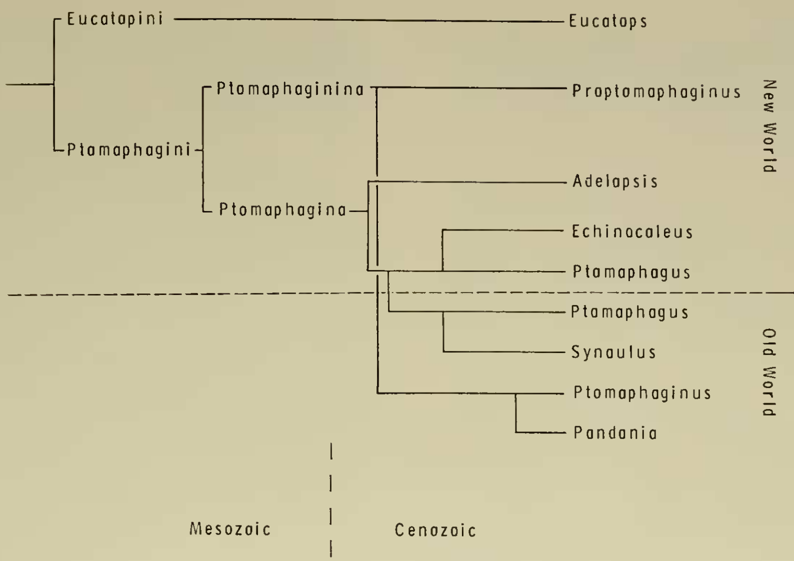


Figure 212. Hypothetical phylogenetic diagram of generic diversification in the tribe Ptomphagini. Degree of generic difference not inferred.

the Americas is in the broad climatic band where north warm temperate and tropical environments merge. This region, grouped as North and Central America including the West Indies, contains four genera, while South America contains only two genera in the tribe. In the past, tropical and subtropical climates existed over much of the North and Central American land masses. These northern lands, rather than South America, were probably the major theaters of early diversification in the Ptomaphagini.

The proto-Ptomaphagini were derived as a line of specialization from the proto-Eucatopini. The aedeagus of the proto-Ptomaphagini became thinner, more elongate and tubular, with the basal blade becoming reduced and fused to the aedeagus.

Within the North or Central American tropics or subtropics, two sublines diverged, perhaps in the late Mesozoic or early Tertiary. The first line, the proto-Ptomaphaginina continued to retain the primitive character of full protibial spination found in Eucatopini. Within the proto-Ptomaphaginina the tendency became established for the migration of the genital orifice to cut the right side of the aedeagus. The second line, the proto-Ptomaphagina, lost the characters of spination on the outer protibial margin. Within this group the tendency became established for the migration of the genital orifice to cut the left side of the aedeagus.

The proto-Ptomaphaginina. While either tropical or subtropical forest conditions prevailed in the early Tertiary, some proto-Ptomaphaginina migrated and spread into the Oriental region, most likely via the continental connection of Siberia and Alaska. These migrant proto-Ptomaphaginina became the genus *Ptomaphaginus*, which spread and speciated moderately throughout the Oriental region. It vanished from more northerly lands in the Old and New Worlds, and a minor lineage led to the development of the monotypic genus *Pandania*. The proto-Ptomaphaginina of the New World undoubtedly were once widespread. Their descendants, in the genus *Proptomaphaginus*, have since be-

come restricted to islands of the West Indies, with only one known species surviving on the mainland (an undescribed cave or soil inhabitant from Mexico). This genus lost the widespread catopine sexual characteristic of dilated protarsi in the males before occupying the West Indies.

The proto-Ptomaphagina. This group was also spreading throughout the tropical or subtropical forests of the early Tertiary in the New World. Selection was acting to perfect the shift of the genital orifice to the left side of the aedeagus. One subgroup, the proto-*Adelopsis* (the *Adelopsis* of today) spread through Central and much of North and South America. They have descended to today with either little shift in the genital orifice, or with a shift on the left side but at the very apex of the aedeagus. This shift at the aedeagal apex has led to almost monstrous complexities in the aedeagal tip in some species. Jeannel (1964) interpreted four species with a median orifice (that is, showing little or no shift in the aedeagus orifice to the left) as remnants of a primitive lineage. These four species have a collective distributional center in Colombia and Venezuela, in the northern Andes. Jeannel thought these were evolutionary relicts, which were isolated in their distributional center from Central and South America by Paleocene seaways. Range expansions into South America were possible with the uplift of the Bolivar geosyncline in the late Oligocene. Jeannel did not know of Central American *Adelopsis* and so did not consider when they may have moved out of northern South America into Central America. If proto-*Adelopsis* arose on Central or North American land masses as I suggest, they moved into South America long enough ago to acquire the high amount of diversity the genus exhibits in South America. South American occupation may have been in the Cretaceous as Jeannel suggests, or even as late as the Tertiary. If the latter, dispersal was across one or more barriers of sea water, because there is no evidence to indicate the presence of continuous land connections at this time (Maldonado-Koerdell, 1964).

*The proto-*Ptomaphagus. In the other subgroup of the proto-Ptomaphagina, the proto-*Ptomaphagus,* the orifice shift occurred on the left side of the aedeagus at a distance from the aedeagal tip. This group apparently acquired a dominance (as Jeannel suggested) that allowed it to spread throughout South and North America, and into the Palearctic Region.

Although Jeannel favored a trans-Atlantic crossing, I believe that the shallow seas separating Alaska and Siberia in and near the Bering Strait seem to be a more likely site for Eurasian-North American land connections. It is well documented (Hopkins, 1967) that the Bering Strait region lay above sealevel throughout most of the early and middle Tertiary, and was a region without pronounced climatic zonation. As late as from the late Oligocene to the middle Miocene Beringia lay at the apex of a continuous region of a broad-leaf deciduous (mixed mesophytic) forest encircling the North Pacific Ocean from Japan through Alaska into the northwestern United States. Paleobotanical evidence suggests that a climatic decline in late Miocene broke this forest band. Climatic factors and the opening of the Bering Strait in the late Miocene led to this disjunction and it has continued to the present (Wolfe and Leopold, 1967). However, fossil mammal data suggests that late Tertiary conditions may have been suitable for *Ptomaphagus* movements. Pliocene (Hemphillian) land-bridge conditions were warm temperate, humid, and forested. Early Pleistocene (Blancan) times were temperate, humid, and forested, with some grasslands present. Middle Pleistocene interglacial (Irvingtonian) conditions were an even division between temperate open grasslands and forest (Repenning, 1967).

In summary, conditions were seemingly suitable on many occasions for the ex-

change of *Ptomaphagus* between North America and Eurasia. If more than one movement did occur is not now evident and will not be so until the Eurasian *Ptomaphagus* are reviewed. It is noteworthy that I have interpreted the movement as being from North America into Eurasia. This is contrary to the general zoogeographic observation that net faunal movements have been from Eurasia into North America.

No matter what else happened, the presence of *Ptomaphagus germari* in Baltic Amber, if correctly determined, indicates that the genus had differentiated and reached northwestern Europe by the Oligocene. This is the only nonspeculative statement that I can make in the entire model of the history of the tribe.

There is only one other paleontologically based statement that can be made about evolution and differentiation in the entire subfamily Catopinae. It is that another Baltic Amber catopid is indistinguishable from *Nemadus colonoides,* which today inhabits much of Europe (Jeannel, 1942: 192). The genus today has only this and one other (Japan) Old World species. Elsewhere, only eleven species are known from the United States and Canada.

The genus *Synaulus* of North Africa may have originated with a middle Tertiary entry of a European *Ptomaphagus* into the habitat of ant nests. Another invasion of ant nests by an early *Ptomaphagus* stock occurred in North America and led to the development of the genus *Echinocoleus.*

The subgenera. The Palaearctic *Ptomaphagus* have been isolated from those of the Nearctic since the time when the Bering Bridge became unsuitable for *Ptomaphagus* dispersal. This may have been in the late Miocene as indicated above. Under present climatic conditions, the northern limits of the range of the genus lie far to the south of Beringia (Map 21). Past Pleistocene interglacials may or may not have been favorable for *Ptomaphagus* migrations between the two regions, depending on the suitability and continuity of forests. Any conclusions about the relationships of Old and New World *Ptomaphagus* can not now be firmly made. A comparative study of Palearctic *Ptomaphagus* is needed.

At present it seems that differentiation in the Palearctic Region has occurred to such an extent that subgeneric separation is possible, but with difficulty. The Eurasian group differentiated into the subgenus *Ptomaphagus* after its isolation from North America. The ancestral stock that invaded Eurasia is indicated below. No evidence is yet at hand to indicate either more than one dispersal into Eurasia or any reinvasion into North America. The difficulty of distinguishing the Eurasian subgenus *Ptomaphagus* from the North American subgenus *Adelops* may indicate a relative recency of separation. The distinct European subgenus *Merodiscus,* now restricted to the Balkans, probably came from Eurasian *Ptomaphagus* before they themselves had been separated from the New World *Ptomaphagus.*

In North, South, and Central America two subgenera are recognized. One of these, *Adelops,* is probably the ancestor of the other three subgenera. *Adelops* has three species groups, each with a more complex spermatheca. I interpret the increasing complexity as an evolutionary trend from primitive to advanced condition. The most advanced species group of *Adelops* is the *cavernicola* group, which today is most abundant in Mexico. The similarity of the spermatheca of the Eurasian *Ptomaphagus* (the few species I have examined) to *cavernicola*-group *Adelops* suggests that *cavernicola*-group *Adelops* were ancestral to the stocks that migrated into Eurasia and differentiated into the subgenera *Ptomaphagus* and *Merodiscus.* The spermathecal similarity between *cavernicola*-group *Adelops* and the Neotropical subgenus *Tupania* (of Mexico and Brazil) similarly suggests that *Tupania* originated from this group of *Adelops.*

Species groups. I have based my species

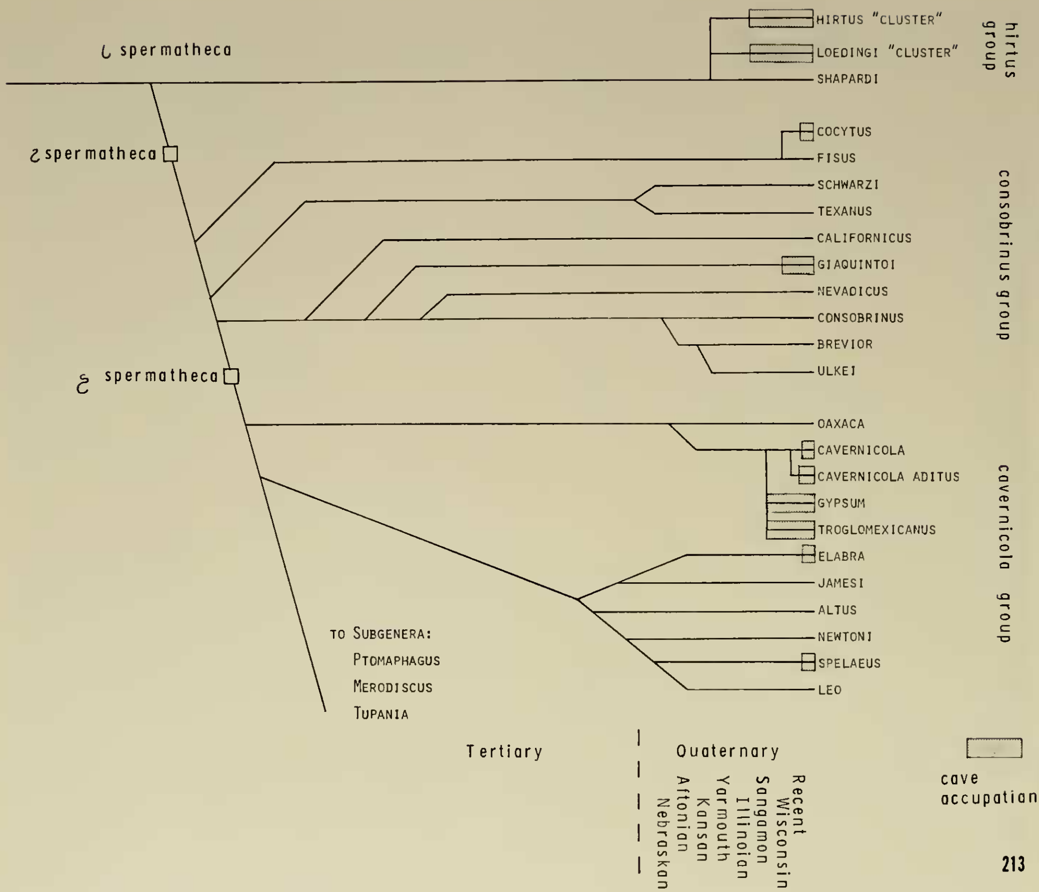


Figure 213. Hypothetical phylogenetic diagram of specific diversification in *Ptomaphagus* (*Adelops*). Degree of specific difference not inferred. Rates of divergence in Tertiary not inferred.

groups in the subgenus *Adelops* upon the female spermatheca, their characters and complexities. This is the only character I found that provided me with data I could use in interpreting a phylogeny for major events within the subgenus. In the discussion to follow only North and Central American events will be considered.

I want to caution here against a too ready acceptance of the chronologic implications of the following discussion. Where I suggest, for instance, that two related events occurred in the Illinoian and Wisconsin respectively, more definitely "earlier" and "later" are being indicated. This is based upon the assumption that greater differences take a longer time to develop than lesser ones. I offer definite times only as appealing possibilities that seem to be logically consistent within an overall framework of combinations of fact, theory, and circumstantial evidence. Figure 213 presents a summary of the following discussion.

I believe the *hirtus* group to be the most primitive, and I base this belief solely upon the observation that within this group the female spermatheca is the most simple, and is closest in form to the other genera in the Ptomaphagina (*Echinocoleus* and *Adelopsis*). The *hirtus* group is hence the oldest of the species groups of *Adelops*,

and I interpret it as being the oldest in the entire genus. At some time, one line of epigean ancestors in the *hirtus* group underwent extreme morphological specialization after occupying deep (montane) forest litter environments. This line acquired behavioral, physiological, and morphological characteristics frequently found in montane soil beetles (edaphophiles). Some of the latter are reduction in pigmentation and cuticle thickness, loss of wings, and reduction of eyes. Selection for these are considered by Darlington (1943, 1970). This line is the only one of the *hirtus* group that has survived. The original epigean species and perhaps several edaphophilic species became extinct. The epigean extinctions may have been in the Tertiary and the edaphophilic extinctions during the warm-dry interglacials of the Pleistocene. Only one edaphophile in the group (*shapardi*) exists today. At a time in the Pleistocene, I suggest the Yarmouth interglacial, two edaphophilic species entered into cave habitats where they underwent further selective change. These have survived until today as troglobites. This cave occupation will be considered below. No species are now known that can be considered close to the ancestral species from which the *hirtus*-group troglobites descended. The possibility exists that continued searching in the southern Appalachian Mountains may uncover an extant edaphophilic species whose ancestors gave rise to the troglobites in the Pleistocene. This would parallel the recent discovery of an epigean *Pseudanophthalmus* carabid which led to a strengthening of conclusions regarding some of the cave species (Barr, 1967b).

Probably early in the Tertiary the *consobrinus* group arose with a spermatheca of intermediate complexity from the *hirtus* group (Fig. 213). The *consobrinus* group spread over North and Central America (or at least into Guatemala), and may have migrated into Eurasia (judging only from the external similarity of *brevior* and *consobrinus* to some European species). The group at least spread over all of the range of the older *hirtus* group and may have been instrumental in the extinction of *hirtus*-group species from the epigean habitats that they undoubtedly occupied. Speciation and range adjustments in the group were undoubtedly intensified during the increased continental drying in the Pliocene and the climatic fluctuations of the Pleistocene. Probably during the drying some species in the west took up their association with various other animals, at first using the nests and burrows of these animals in a facultative way as favorable microclimatic retreats. The group became dominant in America north of Mexico and still is so. Perhaps as late as the Pleistocene it was eliminated from Mexico and Central America except for *nevadicus* and *fisus* in arid western Mexico, and for *giaquintoi*. This last species first persisted in the mid-montane forests of Guatemala, and was eventually restricted to caves in the limestone mountains of eastern Guatemala. The elimination of *consobrinus*-group species from mesic forests in Mexico and Guatemala was possibly related to the rise and spread of the third species group in this region.

The third group, the *cavernicola* group, with the most complex spermatheca evolved from the *consobrinus* group, perhaps in the United States and perhaps in the early Tertiary (Fig. 213). I have already suggested that the other three subgenera of *Ptomaphagus* arose from this group. If this is true, the origin, evolution, and dispersal occurred early enough in the Tertiary to allow their occupation of the Baltic Amber forests. Lately, one species, *cavernicola,* under the opportunities offered by fluctuating Pleistocene (Wisconsin glacial) climates, extended its range from Mexico into and through much of the eastern and southern United States.

Speciation. My attitudes on insect species in the Pleistocene are conservative. They are mostly based upon recent liter-

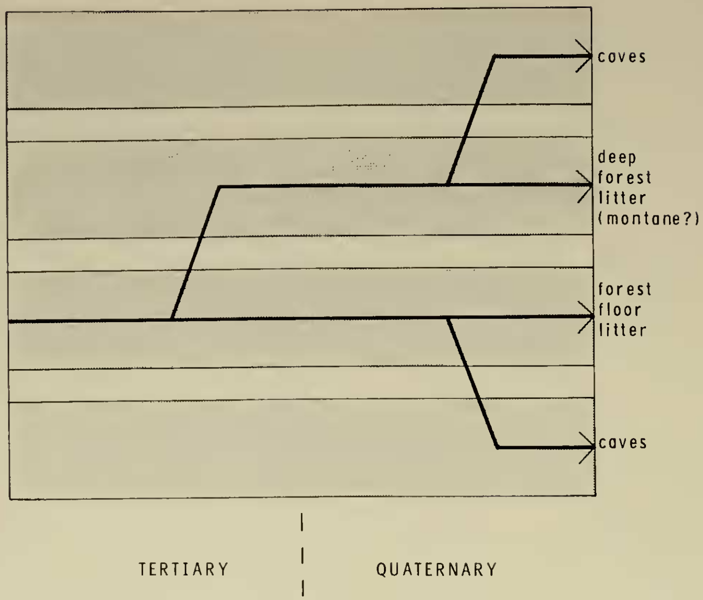


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Figure 214. Hypothetical shifts in adaptive zones in the evolution of *Adelops*, demonstrating the two pathways to cave occupation and specialization. From the ancestral forest floor litter habitat early *hirtus* group ancestors became specialized to deep forest litter, probably in montane situations. Specializations to the new zone resulted in loss of wings and a reduction in the eyes. The morphological and ecological specializations for deep montane litter preadapted the beetles for survival in caves. The deep litter species lived in the cave regions during the Illinoian glaciation. The caves become refuges during the increasing heat and aridity of the Sangamon interglacial. Speciation in the cave populations followed the Sangamon extinction of local epigean populations. The second route of cave occupation (lower zone) involved only ecologically preadopted ancestors in the *consobrinus* and *cavernicola* groups. This lower zone also includes cavelike situations such as mammal burrows.

ature on the problem such as H. H. Ross (1965), Frey (1965), Howden (1969), Coope (1970) and other papers referred to in these works. Generally, these authors agree that insect speciation in the Pleistocene has been of limited extent, except where a combination of unusual ecological requirements and situations has allowed the splitting of populations into smaller isolated units as a consequence of climatic fluctuations. The invasion of caves by *Ptomaphagus* has been one of these unusual situations and has resulted in considerable speciation. There is little that suggests to me that speciation occurred in epigean *Ptomaphagus* in the Pleistocene, but I do accept its possibility, especially for the difficult complex of species in the *cavernicola* group in Mexico.

Speciation in the hirtus *group.* In this group, no wide-ranging, epigean species have survived. The only nontroglibitic species is *shapardi*, a small-eyed, wingless, soil inhabitant of the southwestern Ozark region. This species can be taken as representing the level of morphological specialization possessed by at least two other edaphophilic species of the group in the Tertiary. During the Pleistocene, or before, all epigean species became extinct, one edaphophile survived as such, and two others became cave inhabitants. The route of cave occupation, from preadapted edaphophilic ancestors, under the influence of climatic changes in the Pleistocene, is adequately presented by Barr (1967a, 1968). Figure 214 shows the proposed shifts in adaptive zones experienced by the

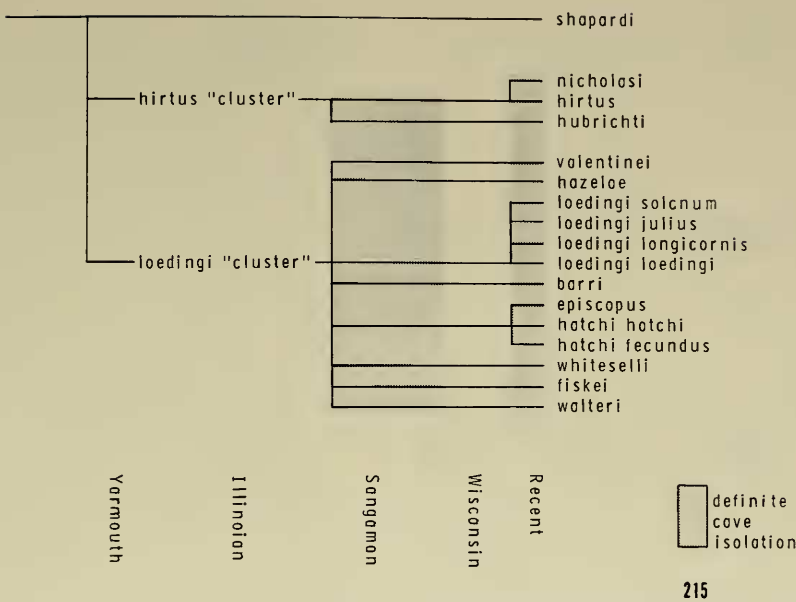

Figure 215. Hypothetical diagram of specific diversification in the *hirtus* group of the subgenus *Adelops*. See text for explanation of possible periods of alternating cave restriction and overland dispersal. Degree of specific difference not inferred.

hirtus group, from the primitive zone as a general forest litter inhabitant into an obligate inhabitant of the zone of deep (montane?) forest litter. As they became specialized for this second adaptive zone, *hirtus*-group members became preadapted (in the sense of Mayr, 1963: 593) for the cave occupation which occurred later in the Pleistocene, just as Barr (1965, 1967b) proposed for the cave occupation of trechine carabid beetles.

When did the cave occupation occur? Only three observations lead me to believe that the *hirtus* group did not invade caves before or after being forced to by the drying-warming trends of the Sangamon interglacial. All the cave species have eye remnants. I think these would have disappeared if the cave occupation had been in the earlier Yarmouth or Aftonian interglacials. Secondly, I would expect surviving montane populations of ancestral descendants if the cave occupation had been early in the present interglacial, but none have been found. Lastly, range sympatry does not exist and it might be expected to occur from additional dispersal opportunities if the initial cave invasion was in the Yarmouth.

Within the *hirtus* group, there are two distinct clusters of troglobitic species (Fig. 215). One, the *hirtus* cluster, is composed of *nicholasi, hirtus,* and *hubrichti* from Illinois, Kentucky, and Tennessee. The second group of troglobites, the *loedingi* cluster, is composed of the remaining species in Tennessee, Alabama, and Georgia. I think these species clusters represent cave occupation by two separate ancestral species. The ancestor of the *hirtus* cluster was more northern in distribution than the ancestor of the *loedingi* cluster.

The former ranges of the ancestral species of the *hirtus* and *loedingi* clusters is a problem. It might be expected that they inhabited the higher forests of the Appalachians, and were able to extend their ranges over the cave-containing lowlands during the Illinoian glacial maximum.

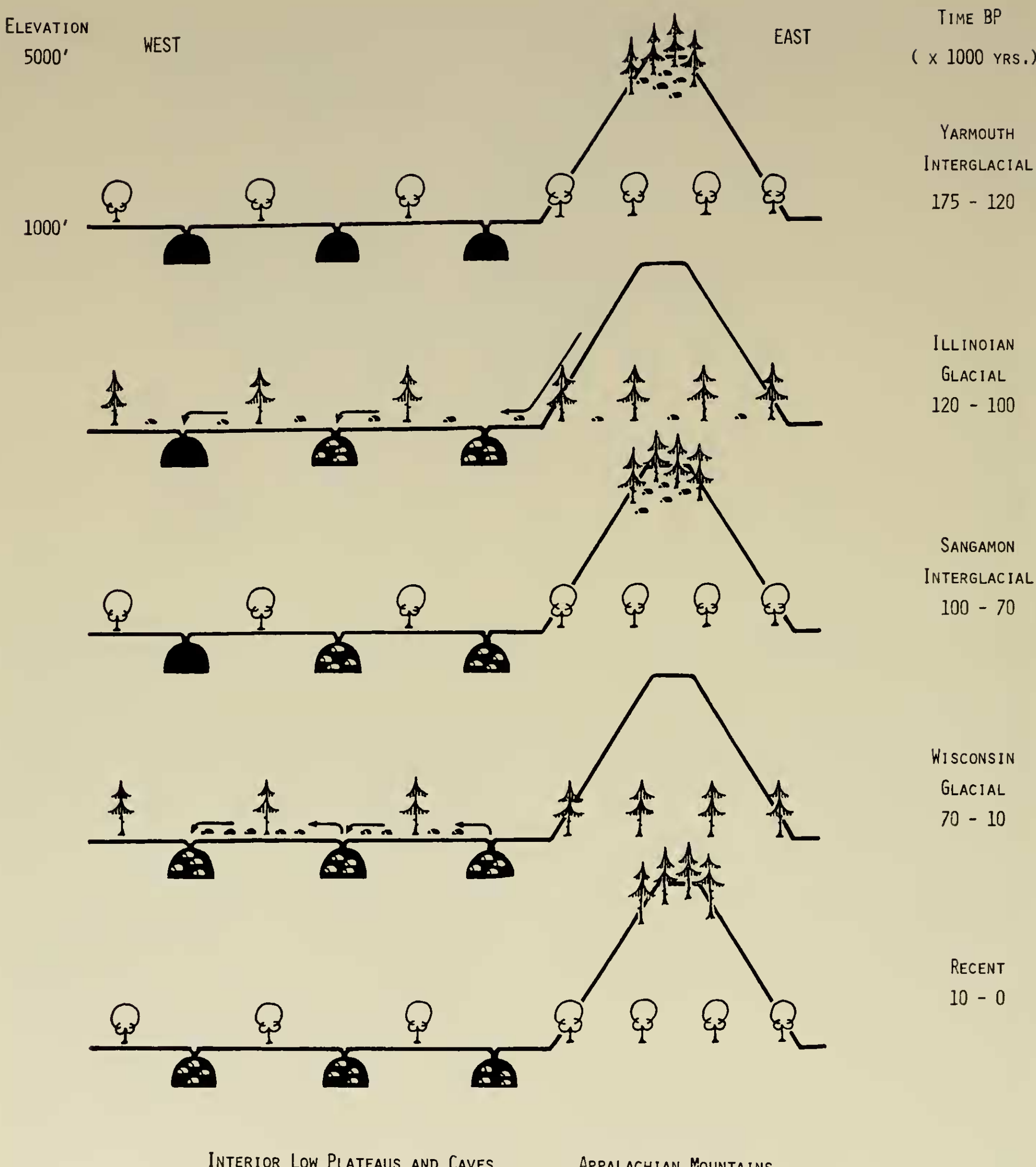

Figure 216. Pictorial diagram of *Adelops* populations movements in the southeastern United States in response to climatic changes in the Pleistocene. This model uses fluctuating Pleistocene climates as a mechanism to introduce the preadapted montane ancestors to cave areas and caves and then to isolate them there. The isolation permitted the development of troglobitic species, which seemingly later underwent range adjustments by overland dispersal in the Wisconsin. Further explanation in text and with Fig. 214. Application of names is a fit of the model to the classical divisions of the continental North American Pleistocene. Times of glacials and interglacials from Emiliani (1971), based on oceanic sediments. This application is controversial, and simplistic. Its effect here is to perhaps make too rapid the speciational and adaptational events. Biologists often do not appreciate the fact that, for purposes of interpreting evolutionary events and biogeography in a framework of Pleistocene history, the use of a time scale matched with climatic conditions and classical Pleistocene division names preceding 150,000 years BP is presently very questionable (see Broecker, 1965).

But this seems less likely when compared with the distribution of the carabid trechine *Pseudanophthalmus* beetles. These beetles probably did move down from higher elevations in the glacials and did occupy the caves at the early stages of the interglacials (Barr, 1967a, 1968). But these carabids occupied caves not only in the flat limestones of Illinois, Kentucky, Tennessee, Alabama, and Georgia where cave *Adelops* occur, but also the flat limestones of Ohio and Indiana, and in even greater regions of Kentucky, Tennessee, and Alabama where cave *Adelops* do not occur. They also occupied the folded-faulted limestones of the Appalachian Valley of Alabama, Tennessee, Virginia, and West Virginia, where troglobitic *Adelops* do not occur. This great difference of geographical ranges of cave occupation between the two genera must lie in one or several of the following comparative reasons. 1) The cave-occupying ancestors of the *hirtus* group came from a different geographic area, perhaps from west of the Appalachians during the Illinoian glaciation. 2) There was a great dissimilarity in the overland dispersal abilities of the ancestral beetles. 3) If ancestral *hirtus*-group species did occupy caves in a greater geographic area than they now occupy, they have now vanished (especially in the folded-faulted limestones of the Appalachian Valley) because their ecological requirements and/or population structure were unsuitable and insufficiently adaptable. This last seems to me to be less likely than the first two.

Distributional events in the *loedingi* cluster were undoubtedly complex, and have led to the complicated speciation and distribution now found in Tennessee, Alabama, and Georgia, while the *hirtus*-group events were less complex and led to the speciation and distribution in Illinois, Kentucky, and Tennessee (Fig. 215 and Map 2).

The following model that I propose is summarized in Figure 216. The species ancestral to the *loedingi* and *hirtus* clusters were edaphophiles that may have become isolated at high elevations in forest litter in the Appalachians during the Yarmouth interglacial. During the Illinoian glacial, with a depression of life zones, the wingless edaphophiles spread into the cave-containing lowlands.

What were the Illinoian climatic conditions like? Virtually no information is available from the southeastern United States. Although the climatic conditions in the cave regions of the interior low plateaus during the Illinoian are unknown, they may be inferred from what is known of a nearby Wisconsin site in Bartow County, Georgia, about 40 air miles from the nearest *Adelops* cave and 100 air miles SE of Huntsville at the western edge of the range of cave *Adelops* in Alabama. Watts (1970) found that in a full glacial (Wisconsin) environment of 20,100 and 22,900 years BP Bartow County harbored a floral assemblage characteristic of sites today lying 1,100 km to the north in New England. It seems reasonable to assume that the climate, causing the vegetational changes, might have been similarly changed in the nearby cave region of northeastern Alabama and adjacent states that is comparable in elevation and latitude to the Bartow County site.

Even if the Illinoian climate was not comparable to the Wisconsin, the beetles distributed themselves into at least parts of the cave-containing regions of the interior low plateaus. Some populations entered caves, found conditions suitable for survival, and became facultative troglophiles. As the Illinoian ice vanished and the warmer and drier conditions of the Sangamon interglacial came into being, the epigean environment became increasingly unsuitable for the lowland epigean populations. Perhaps some of them moved back up the mountains. At this time in the early Sangamon the opportunities were restricted for overland dispersal and gene flow between cave-inhabiting populations, and then they were eliminated by a gradual

extinction of the epigean populations. The populations of facultative troglophiles then became isolated genetic entities, and each could genetically try to respond in its own way to the selective pressures of the caves. The "genetic size" of each population depended on the availability of food to support its individuals, and the extent of continuous underground dispersal corridors. At this time some or most of the cave populations may have become extinct. However, some persisted, and in the process of meeting the rigors of survival as small cave-limited populations they became obligate troglophiles. As divergence and adaptation proceeded throughout the Sangamon, the troglophiles progressed to the troglobitic level of specialization, sometime before the Wisconsin glaciation.

At the beginning of the Wisconsin, then, the *hirtus*-cluster ancestor had split into *P. hirtus* occupying caves in Kentucky, and *P. hubrichti* in caves in Tennessee. The *loedingi*-cluster ancestor had split into *P. barri* in central Tennessee, and *P. valentinei, hazelae, loedingi, whiteselli, fiskei, hatchi*, and *walteri* in caves along parts of the edge of the Cumberland Plateau in Tennessee, Alabama, and Georgia. The caves occupied at the beginning of the Wisconsin are judged to be close to or the same caves as are occupied now for the simple reason of the observed tight distributional pattern now observed. A more confused or elaborate distribution would seem likely if the Sangamon distribution was much different from that of today. Thus, the major features of distribution and speciation in the cave *Adelops* of the southeast were established by the beginning of the Wisconsin.

However, some minor features of distribution and morphological differentiation may have been acquired more recently. It seems possible that the full Wisconsin glacial climatic conditions in the cave regions may have been suitable for the overland dispersal of the recently evolved troglobites (see the above discussion of the full glacial environment in Bartow County, Georgia). Such minor features might be the spreading of *P. loedingi* eastward across the Flint River into Keel Mountain, and then eastward across the Paint Rock River into July Mountain and Tater Knob, leading to the later geographic isolation and subspeciation of these populations in the present interglacial. Similarly, *P. hatchi* may have spread northwestward into Caney Hollow Cave, to become later isolated, thereby accounting for its acquisition of subspecific differentiation. *P. episcopus* is close enough to *P. hatchi* that it may represent the descendants of a *hatchi* occupation of Bishop Mountain during Wisconsin range expansions. Also, the complex pattern of spermathecal forms in *hatchi* may date from multiple dispersals and colonizations at this time. This may also be the time that *P. whiteselli* dispersed across Wills Creek in Lookout Valley, but no morphological differences exist between populations from both sides of the valley.

The wide range of *P. hirtus,* on both sides of two major rivers potentially acting as dispersal barriers in Kentucky, may date from Wisconsin overland dispersal. The lack of differentiation between *hirtus* and *nicholasi* may represent a migration of *hirtus* from Kentucky into Illinois during the Wisconsin. Conditions in caves in Illinois in the Wisconsin may have been too rigorous during the glacial maximum for the survival of descendants from a Sangamon colonization because of the proximity of the ice front (Map 2). Cave occupation by *hirtus* in Illinois was probably during the Wisconsin glacial recession.

Distributional data supporting the Wisconsin overland dispersal of *Ptomaphagus* is also available for *Pseudanophthalmus* carabid beetles. Close morphological similarity and great geographical separation occur in these carabids in several species pairs such as *englehardti* and *loedingi* (Krekeler, 1959), *hoffmani* and *petrunkevitchi* (Barr, 1965), and *illinoisensis* and *barberi* (Barr and Peck, 1966).

Although I think the possibilities were good for overland dispersal of the cave species during the cooler (perhaps more moist) climates of the Wisconsin glacial maximum, the hypothesis is somewhat weakened by the fact that no remnant population from this dispersal is now known to exist in a noncave habitat. I think this is somewhat strange, because the southern and middle Appalachian Mountains harbor a wealth of cavelike habitats in their cool, wooded, wet and rocky gorges and ravines. If the post-Wisconsin altithermal (or hypsithermal) affected the Cumberland Plateau, it may have helped to eliminate any such remaining epigean populations. The possibility of discovering a relict population from this dispersal is brightened by the recent discovery of a remnant epigean population of *Pseudanophthalmus* in West Virginia (Barr, 1967b).

Of great ecological interest is the observation that divergence in the troglobitic *Pseudanophthalmus* of the eastern United States has led to the development of about 165 species (Barr, 1969), contrasted with the 12 cave species of *Adelops* in the same area. In many cases two and up to five (in Mammoth Cave) species cohabit single cave systems. Ecological problems of niche separation and resource division may be pertinent to these trechines, but are not pertinent to cave *Adelops,* because no specific sympatry is known for them. This observation again argues for the greater multiplicity of speciational and distributional events over a greater time period for *Pseudanophthalmus* than for *Adelops.*

If overland dispersal was possible for the troglobitic *hirtus*-group *Adelops* in the cooler Wisconsin climates, it is not now possible. Present dispersal is limited to subterranean routes. The availability of such pathways and avenues is dependent upon the previous courses of ground-water solution in the cave-bearing limestones. For the *loedingi* species cluster these dispersal avenues are now only in limestones at the flanks of the Cumberland Plateau and the Highland Rim. Subterranean dispersal is not possible for these beetles through the water-filled spaces in the limestones underlying lowlands and river valleys. Likewise, dispersal is generally not possible under the Cumberland Plateau through the limestones underlying the Pennington and Pottsville shales and sandstones, but exceptions may exist. I know of no geological references on this point, but it seems to be a widely held geological assumption that groundwater flow in the limestones under the Pennington and Pottsville of the Cumberland Plateau is virtually nonexistent. If groundwater flow (not deep artesian flow) has formed solution channels under the Pennington-Pottsville, these channels have not yet been discovered. Thus, my range maps show the Cumberland Plateau as a dispersal barrier. However, the situation is different in Kentucky where large cave systems such as Mammoth Cave have been developed under a sandstone caprock.

Active dispersal by these wingless cave-beetles is, of course, limited to walking through their subterranean corridors. Passive dispersal in the caves seems likely only by means of flood waters, which usually occur in the winter and spring. Floods probably only infrequently carry individuals to as yet uncolonized sections of the same cave system. The chances for flood waters carrying an individual to a new and uncolonized cave system are even lower. That this is nevertheless a possibility, and that its success depends upon the beetles ability to withstand submersion, is discussed by Barr and Peck (1965) in their consideration of a cave carabid beetle found washed from an Alabama cave.

Speciation in the consobrinus *group.* Little can be offered as a series of speciation and distributional events for this group (Fig. 213). Perhaps more than one species adapted to the Pliocene drying of the western United States by entering protected habitats such as animal burrows. This is seen in the wide western distribu-

tion of *fisus* and *nevadicus* in moderate to very xeric regions. In the late Pleistocene (Sangamon interglacial?) a population of *fisus* became isolated in, and adapted to, a cave in Arizona, differentiating into *cocytus*. Some type of isolation probably acted to produce the elytral variation in *nevadicus*, with the Pacific Northwest populations retaining striae typically oblique to the elytral suture, while the populations over the rest of the range diverged toward striae that were transverse to the suture. The disruption of the trans-continental mesic forests which began in the Miocene probably separated *californicus* from the rest of the *consobrinus* cluster of species. This progressive drying also led to the restriction of the ancestor of *giaquintoi* to the more moist parts of Mexico and Central America. It is now restricted to caves and probably entered the cave-adaptive zone without experiencing much morphological specialization but with at least some ecological specialization acquired in the deep forest litter adaptive zone (see Fig. 214). An early Pleistocene event (interglacial?) may have separated the ancestor of *consobrinus* from that of *brevior* and *ulkei*, these last two diverging later. Variation in *brevior* comes from a later Pleistocene event.

Speciation and dispersal in the cavernicola *group.* The story in this group is more complex than is here indicated (Fig. 213), because of the number of species in the group not yet described. Its distribution is presently in association with the moist mid-montane forests of Mexico and Guatemala, with only one species known from outside this tropical region. Members are unknown from lowland tropical forests. For reasons given above, this group is the most advanced, the youngest to develop, and the ancestor from which arose the other three subgenera of *Ptomaphagus*. As previously indicated, the time of origin must have been in the early Tertiary if not before. Up to mid-Tertiary times there were forest corridors for migration between the north and the forests at the edge of the Mexican Plateau. Probably the *cavernicola*-group ancestors moved southward with the warm-temperate forest element that had reached Mexico by the mid-Tertiary (Martin and Harrell, 1957). This montane Mexican forest today has a marked affinity to the flora of the eastern United States (and also to a lesser degree to that of southeastern China). The disjunction of the flora by the Pliocene development of an arid zone in southern Texas and northeastern Mexico also marked the disjunction of the *cavernicola* group and it perished to the north of this arid zone, leaving no hint about a possible region of origin in the form of relict species.

The oldest cluster of species in the group is the *cavernicola* cluster. It originated from a montane ancestor that had become morphologically and ecologically adapted to montane forest litter. A survivor of this ancestor is the species *oaxaca* living in the eastern mountains of the Mexican State of Oaxaca. An undeterminable speciation event gave rise to what was to become the species *cavernicola*. At least two populations of early *cavernicola* were isolated in cave habitats in the early Sangamon interglacial. One of them, *troglomexicanus*, became more modified for cave existence than the other, *gypsum*. During the Wisconsin glaciation, *cavernicola* itself spread northeastward out of Mexico across the arid zone of northeastern Mexico and southern Texas. This zone had become ameliorated enough so that savanna conditions existed (Martin and Harrell, 1957). Temporary use of animal burrows may have aided the crossing of this barrier, since caves are absent here. When *cavernicola* reached central Texas it encountered mesic forests and caves, and the way was clear for it to disperse to at least the extent of its present range. This present range is undoubtedly one of (altithermal?) contraction, because the species is now known mostly from caves, which are undoubtedly being used as some sort of refuge. Temper-

ate forests may presently be inadequate in some way for permanent occupation. The lack of material from forests may also indicate an unusual seasonality of overland flight and dispersal, judging from the one South Carolina forest collection made in the wintertime. One population of *cavernicola* has been out of the mainstream of genetic contact long enough that it has acquired enough differences to be treated as the subspecies *cavernicola aditus*, inhabiting Cueva de la Boca, south of Monterrey, Mexico. This probably results from a longer period of population isolation, beginning with the early return of the present arid conditions in northeastern Mexico. It is interesting that the other known Mexican population from Gruta del Palmito, north of Monterrey, has not diverged, although it has seemingly also suffered the same isolation.

Little or nothing of a positive nature can be offered concerning the times and places of speciation events in the remaining six named species in the group. The position of *elabra* is isolated because of the unusual shape of the anterior end of the spermatheca. The species *jamesi* is closer to *altus* in features of the spermatheca and aedeagus than it is to *newtoni*, but *newtoni* and *jamesi* are not pruinose near the rear of the female elytral suture, which *altus* is. The species *leo* and *spelaeus* have similar spermathecae but are different in aedeagal characters, with *spelaeus* females having the pruinose elytral tip, which is absent in *leo*.

The cave occupation of *elabra* and *spelaeus* probably dates from the Wisconsin. At that time populations moved down from higher elevation forests. With the Wisconsin recession the lowland populations were left in cave refuges as the climate became drier or hotter. The species undoubtedly exist today somewhere in nearby epigean environments.

There are certainly more than the present ten named and seven unnamed species in the *cavernicola* group. This is evident simply because so few collectors in Mexico have used the specialized methods necessary for collecting Catopinae. How can we account for the production of this close-knit group of at least 17 species with its center of abundance in the mid-montane forests of eastern Mexico? It might be viewed simply as a manifestation of the generalization of a higher species diversity in tropical regions compared to temperate regions. However, this cannot be the case, because the mid-montane forests are actually temperate in their physical and biological characteristics. As a model for explaining the high species diversity I suggest a modification of that offered by Martin (1955). He noted that an isolated patch of Mexican cloud forest (at Rancho del Cielo, Tamaulipas) did not have any vertebrate species that were limited to it. He suggested that if any obligate cloud forest vertebrates did inhabit it in the past, they may have been eliminated by reduction of forest size under different climatic circumstances. However, the forest reduction (or reductions) were not severe enough to reduce the richness of the floral components. If there was such a period of fluctuating boundaries with disjunctions and reunions in the mid-montane forests, this offers an excellent model for multiple geographic isolations in the insect fauna. It suggests that much endemism can be expected by future students investigating the terrestrial arthropod fauna of these forests. However, if this fauna is to be known, active and intense efforts must be made now to collect it, because the destruction and disruption of these forests for domestic and agricultural purposes is proceeding at a very rapid rate.

Conclusion and prospectus. In closing the discussion of the phylogeny and zoogeography, I believe it is useful to restate three of the major operational assumptions I have used. 1) That the group that I call the tribe Ptomaphagini arose in tropical-subtropical America, probably on the land mass that is now North or Central America. 2) That the morphology of the spermatheca

of *Ptomaphagus* is useful for uniting species into groups. 3) That I have correctly interpreted the progression of evolution in the spermatheca from simple to complex as an indicator of the relative ages of the species groups. Proceeding from this basis, I have constructed the above past history for the group in a manner that I believe is internally consistent for the data available. I offer the history as a model that can be continually tested as new data become available, in the form of new taxa, characters, and distributional information.

I believe it will be an interesting future exercise to test the phylogenetic scheme with phenetic (numerical) and cladistic methodologies. In the former the anticipated difficulty will be the discovery of a sufficient number of unit characters that can be coded as "0" or "1." The difficulty of the latter will be in making decisions on the primitive and advanced conditions of each character. In such an endeavor the greatest aid comes from comparing conditions in the unit under study with those in allied groups. This I have already done in many instances in arriving at the above reconstructed evolutionary history.

Lastly, it is interesting to note as a general summary and conclusion that multiple cave occupation and specialization has occurred in all three species groups of *Ptomaphagus* and occurred to at least nine ancestral species which resulted in nineteen cavernicolous species. Some of these nineteen are more cave adapted than others. None of the original cave occupations occurred before the beginning of the Sangamon interglacial. The levels of adaptation and specialization in troglobitic *Ptomaphagus* are far below the levels achieved by the troglobitic Bathysciini of Europe.

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Valid generic names and specific combinations in italics; only major discussions listed for species